Neural and Behavioral Responses to Attractiveness in Adult and Infant Faces

Amanda C. Hahn[1] & David I. Perrett[2]

[1] University of Glasgow, Institute of Neuroscience and Psychology
[2] University of Saint Andrews, School of Neuroscience and Psychology

Corresponding Authors:
Amanda C. Hahn
Institute of Neuroscience and Psychology,
University of Glasgow
58 Hillhead Street
Glasgow, G12 8QB
Email: Amanda.Hahn@glagsow.ac.uk

David I. Perrett
School of Neuroscience and Psychology,
University of Saint Andrews
St Mary's Quad
Saint Andrews, KY16 9JP
Email: dp@st-andrews.ac.uk

ABSTRACT

Facial attractiveness provides a very powerful motivation for sexual and parental behavior. We therefore review the importance of faces to the study of neurobiological control of human reproductive motivations. For heterosexual individuals there is a common brain circuit involving the nucleus accumbens, the medial prefrontal, dorsal anterior cingulate and the orbitofrontal cortices that is activated more by attractive than unattractive faces, particularly for faces of the opposite sex. Behavioral studies indicate parallel effects of attractiveness on incentive salience or willingness to work to see faces. Both work/effort and brain activation to the sight of opposite sex attractiveness is more pronounced in men than women, perhaps reflecting the greater importance assigned to physical attractiveness by men when evaluating a potential mate. Studies comparing heterosexual and homosexual observers indicate the orbitofrontal cortex and mediodorsal thalamus are more activated by faces of the desired sex than faces of the less preferred sex, independent of observer gender or sexual orientation. Infant faces activate brain regions that partially overlap with those responsive to adult faces. Infant faces provide a powerful stimulus, which also elicits sex differences in behavior and brain responses that appear dependent on sex hormones. There are many facial dimensions affecting perceptions of attractiveness that remain unexplored in neuroimaging, and we conclude by suggesting that future studies combining parametric manipulation of face images, brain imaging, hormone assays and genetic polymorphisms in receptor sensitivity are needed to understand the neural and hormonal mechanisms underlying reproductive drives.

Keywords: facial attractiveness; neural correlates; reward; motivational salience; face processing; sex differences

Glossary of terms and abbreviations

Imaging technique terms:
PET – positron emission tomography
fMRI – functional magnetic resonance imaging
MEG – magnetoencephalography
EEG – electroencephalography
ERP – event-related potential
BOLD – blood-oxygen-level dependent

Brain structures:
FFA – fusiform face area
FG – fusiform gyrus
IFG – inferior frontal gyrus
IOG – inferior occipital gyrus
mdT – mediodorsal nucleus of the thalamus
NAcc – nucleus accumbens
OFC – orbitofrontal cortex
PFC – prefrontal cortex
mPFC – medial prefrontal cortex
vmPFC – ventromedial prefrontal cortex
STS – superior temporal sulcus
SDN – sexually dimorphic nucleus of the preoptic area of the hypothalamus
SLEA – sublenticular extended amygdala
VTA – ventral tegmental area

I. Neural correlates of face perception

Facial perception is an extremely well developed skill among humans – one that is essential for social interactions. We garner a wealth of socially relevant information, such as emotion and familiarity, from the face. Behavioral research has demonstrated that humans rapidly form a number of social attributions, judging the trustworthiness (Stirrat & Perrett, 2010), leadership potential (Re et al., 2013; Rule & Ambady, 2008), and health (Coetzee, Perrett, & Stephen, 2009) of individuals based on their faces alone. Imaging work exploring the neural correlates of face perception has provided evidence that a specialized neural system exists for face perception. This distributed cortical network includes multiple regions (Haxby, Hoffman, & Gobbini, 2002, 2000; Kanwisher, McDermott, & Chun, 1997) and has a degree of functional lateralization to the right hemisphere (Kanwisher et al., 1997).

The face processing system in located primarily in the occipito-temporal cortex in both monkeys and humans (Freiwald & Tsao, 2010; Kanwisher & Yovel, 2006; Perrett, Hietanen, Oram, & Benson, 1992; Tsao, Freiwald, Tootell, & Livingstone, 2006). Early work in humans demonstrated consistent activation of a region of the lateral fusiform gyrus in response to facial stimuli (Halgren et al., 1999; Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997). This 'fusiform face area' may represent a specialized module for facial processing that does not appear to process other categories of objects, despite expertise and familiarity (Grill-Spector, Knouf, & Kanwisher, 2004; though see Bilalic, Lagner, Ulrich, & Grodd, 2011; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Subsequent work has revealed other posterior brain regions that predominantly process facial information (Tsao, Moeller, & Greiwald, 2008).

More recently, and building on Bruce and Young's (1986) model of face perception, Haxby et al. (2000, 2002) have proposed a model comprised of a "core system" and "extended system" (Figure 1). The core system of this model consists of three regions in the visual extrastriate cortex: the inferior occipital gyrus (IOG), fusiform gyrus (FG, location of the fusiform face area or FFA), and superior temporal sulcus (STS). The IOG provides input to the FG and STS, which modulate the representation of fixed aspects of the face such as identity and the representation of changeable aspects of the face such as biological motion, respectively. While the core system is thought to be crucial for the visual analysis of facial stimuli, the extended system is considered a component of the neural network of face processing in that regions within this system are recruited to process the significance of information ascertained from the face. Haxby et al's extended system consists of neural regions associated with other cognitive functions such as attention (i.e., intraparietal sulcus) and speech perception (i.e., auditory cortex). In Haxby's model, key components of the extended system are the insula and what they call the limbic system (i.e. regions such as the hippocampus, thalamic nuclei, fornix, and cingulate gyrus). Haxby et al. posit that the limbic system is involved in emotion perception, which may relate to processing of the social significance of facial stimuli.

[INSERT FIGURE 1 ABOUT HERE]

Because of its effective connectivity with the FFA, the orbitofrontal cortex (OFC) may also be involved in this extended system for face processing (Fairhall & Ishai, 2007). Indeed, face-selective neurons in the OFC have been identified in monkeys

(Thorpe, Maddison, & Road, 1983), and in humans the OFC responds more strongly to images of people than images of non-people (Kawabata & Zeki, 2008). The OFC is a key component of the traditional reward circuitry, implicated in the representation of reward value (Kringelbach & Radcliffe, 2005). Activation in the OFC has been observed during aesthetic judgements (Ishizu & Zeki, 2013; Jacobsen, Schubotz, Höfel, & Cramon, 2006) and the experience of beauty across different sensory modalities (Ishizu & Zeki, 2011), suggesting a potential role for this region in the aesthetic assessment of faces, including judgements of facial attractiveness. In light of research demonstrating activation in brain regions associated with the processing of rewards (e.g., the OFC, prefrontal cortex or PFC[1], nucleus accumbens or NAcc), Senior (2003) proposed an extension of Haxby's model incorporating specific involvement of the reward-system for the processing of facial appearance, especially relevant for the perception of facial attractiveness (Figure 1). See Figure 2 for a visual representation of the anatomical regions described above.

[INSERT FIGURE 2 ABOUT HERE]

While there is strong evidence for the existence of a general face processing system, whether or not all faces are processed in the same fashion remains to be determined. For instance, some behavioral and neuroimaging studies would suggest that an opposite-sex bias in face processing may occur among heterosexual individuals. Electrophysiological studies have demonstrated larger centro-parietal N400s and late positive components (LPCs, sometimes referred to as the late positive potential or

[1] Anatomically, the prefrontal cortex (PFC) comprises the ventromedial prefrontal cortex and frontal pole (BA10), dorsomedial prefrontal cortex (BA9), orbitofrontal cortex (BA11), and parts of the anterior cingulate cortex. These subregions of the prefrontal cortex constitute distinct functional modules (Bzdok et al., 2013; Croxson et al., 2005).

LPP), components which are thought to represent neural responses to meaningful or motivationally relevant stimuli, in response to opposite-sex as compared to same sex faces (Proverbio, Riva, Martin, & Zani, 2010a). These responses are indicative of heighted attention to and/or memory for opposite-sex faces as compared to same-sex faces. Analyses of the intra-cortical source of these responses suggest that many of the neural correlates of face processing may demonstrate these sex-biased activation patterns.

Although there is some evidence that Haxby's core system, particularly the FG (Proverbio et al., 2010a; Turk et al., 2004) and the STS (O'Doherty et al., 2003) may respond more strongly to opposite-sex faces than to same-sex faces in heterosexual individuals, in a study of both heterosexual and homosexual individuals, Kranz and Ishai (2006) found no evidence that stimulus sex modulated face responses in these regions. By contrast, there is more consistent evidence for an opposite-sex bias in activation of neural regions associated with Haxby's extended system. An opposite-sex biased neural response has been observed in the amygdala (Aharon et al., 2001; Fisher et al., 2004; c.f., Kranz & Ishai, 2006), cingulate cortex (Proverbio et al., 2010a; Turk et al., 2004), insular cortex (Fisher et al., 2004; Turk et al., 2004; c.f., Kranz & Ishai, 2006), OFC and regions of the PFC (Ishai, 2007; Kranz & Ishai, 2006; Spreckelmeyer, Rademacher, Paulus, & Gründer, 2012; Turk et al., 2004; c.f., O'Doherty et al., 2003), mdT (Kranz & Ishai, 2006), as well as in additional reward-related structures such as the NAcc (Bray & O'Doherty, 2007) and VTA (Aharon et al., 2001). Together these findings suggest that, among heterosexual individuals, opposite-sex faces may hold greater significance or reward value than same-sex faces.

II. Sexual Dimorphisms in Face Processing

Although the cortical network involved in face processing is bilaterally distributed throughout the brain, a right hemisphere dominance has been observed using a number of imaging techniques including: electroencephalography (EEG, Bentin, Allison, Puce, Perez, & McCarthy, 1996; Halit, Haan, & Johnson, 2000), functional magnetic resonance (fMRI, Kanwisher et al., 1997; McCarthy et al., 1997), magnetoencephalography (MEG, Itier, Herdman, George, Cheyne, & Taylor, 2006; Sams, Hietanen, Hari, Ilmoniemi, & Lounasmaa, 1997), positron emission tomography (PET, Rossion et al., 2000), and single-cell recordings (Perrett et al., 1988).

Interestingly, this right hemisphere lateralization is more apparent in men than in women. Using MEG, Tiedt et al. (2013) investigated sex differences in the M170, which originates from sources within the FG (Deffke et al., 2007; Halgren, Raij, Marinkovic, Jousmäki, & Hari, 2000; Kanwisher et al., 1997), in response to viewing faces. A right-lateralized M170 response was observed in men while viewing faces, whereas women showed a bilateral M170 response to the same stimuli. Similar evidence for a sex difference in lateralization comes from EEG work, which reports larger N170 responses to faces in the right than left hemisphere among men, but no such right-hemisphere dominance among women (Proverbio et al., 2010b). The N170-component is thought to reflect the structural encoding of faces (Bentin et al., 1996) and parallels with the M170 component observed in MEG recordings (Halgren et al., 2000; Liu, Harris, & Kanwisher, 2002). Source localization of this response has indicated that the observed activation originated in the FG, although some other

studies have suggested that the N170 is influenced by sources in other face-responsive regions such as the STS (Itier & Taylor, 2004).

Sex differences have also been observed in lateralization of the P2 component when facial stimuli are presented), however these observed sex differences in lateralization of the P2 response were not linked to attractiveness of the facial stimuli (van Hooff, Crawford, & van Vugt, 2011). Although it is not necessarily face-specific, the P2 component is thought to relate to the emotional significance of stimuli, as it is typically larger for pleasant and unpleasant stimuli as compared to neutral stimuli (Amrhein, Mühlberger, Pauli, & Wiedemann, 2004).

Sex differences in brain anatomy may contribute to the sex difference in the lateralization of face processing. Across a number of brain regions, sex differences have been observed with regards to both structure and function (for reviews, see Luders & Toga, 2010; Zaidi, 2010). These sex differences in brain anatomy may influence a number of cognitive functions such as spatial tasks and verbal memory tasks (Hyde & Linn, 1988; Johnson et al., 2002; Lin & Peterson, 1985; Shaywitz et al., 1995). Such structural and functional differences could lead to sexual dimorphisms in response to faces in general as well as facial attractiveness, specifically. Indeed, women have more white matter than men (Witelson et al., 1995) and a larger corpus callosum (Bishop & Wahlsten, 1997; Leonard, Towler, Welcome, & et al., 2008), which may allow for greater neural transmission between the two hemispheres.

Sexual dimorphism also occurs in the opposite-sex bias for face processing; some studies suggest the opposite-sex bias exists in only one sex or the other, while others indicate that this processing bias may present differently in men and women. For example, men exhibit a larger P2 potential response to opposite-sex faces than same-sex faces over left temporal sites, whereas women exhibit a similar increased P2 opposite-sex face response over central cites (Suyama et al., 2008). Similarly, Spreckelmeyer et al. (2012) found that although there is evidence of an opposite-sex bias in neural responses within the reward circuitry, the effect was larger for men than women in the NAcc but larger for women than men in the VTA while no sex differences were apparent in the vmPFC.

Non-human animal research suggests that hormonal factors, in addition to genetic and environmental factors, influence sexual dimorphism in brain structure and function. Indeed, greater sexual dimorphism is seen in brain regions that show greater levels of sex steroid receptors during cerebral development (Goldstein et al., 2001). For example, the sexually dimorphic nucleus (SDN) of the preoptic area of the hypothalamus, which is involved in mating behavior, is larger in male than female rats (Raisman, 1971), but it is possible to reduce this sexual dimorphism in size by exposing males to the sex steroid hormones estrogen and progesterone (Bloch et al., 1981). Similar hormonal modulation of neural development may also occur in humans in brain regions important for face processing and emotional expressions such as the visual cortex and amygdala. The amygdala develops at different rates in males and females and may be sexually dimorphic due to early androgen influences. Specifically, the superficial nuclei group of the amygdala, which demonstrates coactivation with the insula, IFG, and NAcc, may influence sexually dimorphic

responses to faces as this region has been implicated in the processing of social stimuli and is linked to olfactory areas important for the processing of reproductive cues such as pheromones (Bzdok et al., 2013).Additionally, both the visual cortex and the amygdala are densely populated with androgen receptors (Hamann et al., 2005; Nunez et al., 2000, 2003). Such differences in androgen receptor density may account for sex differences in basic perceptual processes (Abramov, Gordon, Feldman, & Chavarga, 2012). These hormonally influenced sexual dimorphisms in structural development may contribute to the sexually dimorphic responses observed in the face processing neural network.

III. Neural responses to facial attractiveness

One important form of information ascertained from faces is physical attractiveness. Evolutionary theories posit that the psychological mechanisms underlying attractiveness judgments reflect adaptations that have evolved to aid in the selection of high quality mates. Such a hypothesis is founded upon the notion that physical attractiveness reflects the presence of certain traits or features that are indicative of health or overall mate quality (i.e., cues to both direct and indirect benefits). That perceptions of facial attractiveness show a high level of agreement between individuals, across cultures and age-groups, as well as across the sexes is evidence that preferences for attractiveness may, at least in part, reflect adaptations for social bonding (see Langlois et al., 2000 for meta-analysis). Such agreement does not imply innate preferences since agreement may reflect common learning, yet the faculty of learning itself can be considered an adaptation.

Facial attractiveness has been positively related to reproductive success (Jokela, 2009; Rhodes, Simmons, & Peters, 2005), health and longevity (Henderson & Anglin, 2003; Shackelford & Larsen, 1999), immunocompetence (Jones, Little, Tiddeman, Burt, & Perrett, 2001; Scheib, Gangestad, & Thornhill, 1999), immune function (Klein, 2000; Lie, Rhodes, & Simmons, 2008; Roberts et al., 2005; Roney, Hanson, Durante, & Maestripieri, 2006), and healthy ageing and diet (Fink, Grammer, & Thornhill, 2001; Jones, Little, Burt, & Perrett, 2004; Matts, Fink, Grammer, & Burquest, 2007; Stephen, Oldham, Perrett, & Barton, 2012).

Facial attractiveness strongly influences the impressions we form of unknown individuals. Attractiveness carrys positively valenced stereotypes such as 'what is beautiful is good' (i.e., the attractiveness halo effect; Dion, Berscheid, & Walster, 1972; Nisbett & Wilson, 1977). Indeed, attractive individuals are perceived as more competent (Mobius & Rosenblat, 2006), more intelligent (Zebrowitz, Hall, Murphy, & Rhodes, 2002), more interesting (Berscheid & Walster, 1974), and as possessing more positive personality traits in general compared to unattractive individuals (Snyder, Tanke, & Berscheid, 1977). These perceptions can even influence real world outcomes. Attractive individuals are more likely to be hired (for a meta-analytic review, see Hosoda, Stone-Romero, & Coats, 2003), tend to earn more money (Hamermesh & Biddle, 1994), and experience greater dating success (Walster, Aronson, Abrahams, & Rottman, 1966; Woll, 1986) and social success (Prestia, Silverston, Wood, & Zigarmi, 2002) than their less attractive counterparts.

In light of the marked effects attractiveness can have on social interactions, it is important to determine if facial attractiveness influences face processing. Attractive

faces have been shown to capture attention (Chen, Liu, & Nakabayashi, 2012; Leder, Tinio, Fuchs, & Bohrn, 2010) and bias subsequent cognitive processes (Olson & Marshuetz, 2005) to a greater extent than unattractive faces. EEG studies have shed light on the temporal dynamics of attractiveness processing, indicating that attractiveness may begin to exert effects as early as the structural encoding stage. Early indices of visual processing, including the early posterior negativity (EPN) and N170 components, are modulated by facial attractiveness (Marzi & Viggiano, 2010; Pizzagalli et al., 2002; Schacht, Werheid, & Sommer, 2008; van Hooff et al., 2011; Werheid, Schacht, & Sommer, 2007; Zhang & Deng, 2012). This early effect of attractiveness is apparent over frontal and posterior sites. In addition to the early structural encoding stage of face processing, attractiveness appears to have effects in later stages whereby affective and identity information is extracted from faces. The parieto-central LPC, which is thought to reflect heightened processing linked to motivation and attention, is modulated by facial attractiveness (Johnston & Oliver-Rodríguez, 1997; Marzi & Viggiano, 2010; Oliver-Rodríguez, Guan, & Johnston, 1999; Werheid et al., 2007; Zhang et al., 1995; Zhang & Deng, 2012).

The FG is thought to be the cortical source of the N170 response sensitive to facial attractiveness (Pizzagalli et al., 2002). A number of studies have provided evidence for a positive correlation between facial attractiveness and activation in the FG (Chatterjee, Thomas, Smith, & Aguirre, 2009; Cloutier, Heatherton, Whalen, & Kelley, 2008; Kranz & Ishai, 2006; Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007; c.f., Iaria, Fox, Waite, Aharon, & Barton, 2008; Tsukiura & Cabeza, 2011). Indeed, recent meta-analyses confirmed that increased activation in the FG for attractive faces as compared to unattractive

faces is highly consistent across studies (Bzdok et al., 2011; Mende-Siedlecki, Said, & Todorov, 2013). Activation of the FG also appears to be stronger for assessments of attractiveness than other assessments, such as tallness (Kedia, Mussweiler, Mullins, & Linden, 2013). There is mixed evidence, however, for attractiveness effects within the remaining components of Haxby's core system (i.e., the IOG and STS). While two studies found a positive relationship between IOG activation and facial attractiveness (Kranz & Ishai, 2006; Vartanian, Goel, Lam, Fisher, & Granic, 2013), another found a negative relationship (O'Doherty et al., 2003). Similarly, Kranz and Ishai (2006) found evidence that activation in the STS was modulated by facial attractiveness while Iaria et al. (2008) found that STS activation did not differ for attractive and unattractive faces.

While evidence for the involvement of the entirety of Haxby's core system in the processing of facial attractiveness may be equivocal, there is strong support for involvement of the so-called extended system, including Senior's (2003) addition of reward-related brain structures. While an early study using PET revealed greater activity in the left medial frontal cortex and left insular and orbitofrontal cortices for attractive as compared to unattractive faces (Nakamura et al., 1998), perhaps the most consistently reported finding is increased activity in the OFC for attractive as compared to unattractive faces (Aharon et al., 2001; Bray & O'Doherty, 2007; Cloutier et al., 2008; Hampshire, Chaudhry, Owen, & Roberts, 2012; Iaria et al., 2008; Ishai, 2007; Kawabata & Zeki, 2004; Kim, Adolphs, O'Doherty, & Shimo, 2007; Kranz & Ishai, 2006; Liang, Zebrowitz, & Zhang, 2010; Nakamura et al., 1998; O'Doherty et al., 2003; Smith et al., 2010; Tsukiura & Cabeza, 2011a, 2011b; Winston et al., 2007; Zaki, Schirmer, & Mitchell, 2011). The OFC is thought to index

the reward value of stimuli; activity in this region increases with monetary gain in humans (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001) and with the sucrose content of juice rewards among non-human primates (Roesch & Olson, 2004). Notably, a positive association with attractiveness has most often been observed in the medial region of the OFC, whereas a negative association has been observed in the lateral OFC (Cloutier et al., 2008). This pattern of results is supported by non-face research indicating involvement of the medial OFC in reward and the lateral OFC in punishment (Kringelbach & Rolls, 2004). Additional elements of the reward circuitry responds positively to facial attractiveness; stronger responses have been observed for attractive compared to unattractive faces in the VTA (Aharon et al., 2001; Aron et al., 2005), PFC (inferior PFC and mPFC: Chatterjee et al., 2009; mPFC: Cloutier et al., 2008; ventrolateral PFC: O'Doherty et al., 2003), basal ganglia (caudate: Bray et al., 2007; Pochon et al., 2008, putamen: Liang et al., 2010), ventral striatum (Kampe et al., 2001) and the NAcc (Aharon et al., 2001; Bray et al., 2007; Cloutier et al., 2008; Kim et al., 2007; Liang et al., 2010; Smith et al., 2010' Zaki et al., 2011). The thalamus and cingulate cortex also tend to respond more strongly to attractive faces than unattractive faces (Cloutier et al., 2008; Kawataba et al., 2004; Kranz & Ishai, 2006; Liang et al., 2010; O'Doherty et al., 2003; Pochon et al., 2008; Tsukiura et al., 2011a; Winston et al., 2007), although there is some evidence that the cingulate may respond in a non-linear fashion (Tsukuira et al., 2011a). Similarly, the amygdala appears to respond non-linearly to facial attractiveness, with greater activation in response to highly attractive or highly unattractive faces compared to average faces (Liang et al., 2010; Mende-Siedlecki et al., 2012; Winston et al., 2007), although other studies have observed a positive linear response to attractiveness in this region (Aharon et al., 2001; Iaria et al., 2008; Kranz & Ishai, 2006).

That brain regions associated with reward respond to facial attractiveness suggests physical attractiveness may hold incentive salience (Berridge & Robinson, 2003) and influence behavior. Indeed, Wilson and Daly (2004) demonstrated that men will discount high future rewards in exchange for lesser immediate rewards after viewing attractive opposite-sex faces (i.e., temporal discounting). Some evidence suggests that facial attractiveness may even be a stronger reward stimulus than money; Zeng et al. (2012) found that for men, viewing attractive women resulted in a larger LPC response than winning money did, a result they attribute to the possibility that attractive potential mates may be more direct rewards than monetary gain.

Using an effort-based key-pressing task, Aharon et al., (2001) measured the incentive salience of facial attractiveness in a group of men, while additional groups viewed the same faces during fMRI scanning or provided aesthetic ratings of the faces. General attractiveness effects, whereby greater BOLD responses were observed when contrasting attractive versus unattractive faces, were seen in the VTA, sublenticular extended amygdala (SLEA), and OFC. This attractiveness effect interacted with sex of face, such that the attractive – unattractive contrast was larger for opposite-sex faces than same-sex faces, in the NACC, VTA, and SLEA. Effort expended in the key-pressing task more accurately mirrored the pattern of activation seen in reward-related brain regions (i.e. the interaction between attractiveness and sex of face) than did aesthetic ratings, leading to the conclusion that this key-press task may be an behavioral measure of the reward value of "beauty". Further support for this link between key-pressing behavior and incentive salience comes from work with prosopagnosics (Iaria et al., 2008) and individuals suffering from post-traumatic stress

disorder (Elman et al., 2005). These individuals either suffer from perceptual deficits or anhedonia, both of which should impact the incentive salience of facial attractiveness. Indeed, both groups were found to significantly differ from control participants in that they did not exert greater effort to view attractive as compared to unattractive faces. These data highlight the involvement of a distributed neural network, including both the core and extended systems of Haxby's model, for processing and interpreting facial attractiveness.

Is attractiveness a temporally invariant or a dynamic aspect of facial appearance? The nature of attractiveness as a fixed or fluid aspect of appearance is a question that remains unanswered. Involvement of the core system implies that attractiveness may be a fixed or invariant aspect of faces. In light of the considerable evidence that the extended system, including Senior's (2003) addition of reward-related structures, also responds differentially to facial attractiveness suggests that attractiveness may be a variable aspect of faces. Indeed, there is behavioral (Jones, Debruine, Little, Conway, & Feinberg, 2006; Main, DeBruine, Little, & Jones, 2010; Quist, DeBruine, Little, & Jones, 2012) and neurobiological (Kampe, Frith, Dolan, & Frith, 2001; O'Doherty et al., 2003) evidence that facial attractiveness is not simply a consequence of aesthetically pleasing characteristics, but rather an integration of multiple cues including physical appearance, inter-personal engagement, and emotional expression.

It is notable that the neural correlates of the processing of facial attractiveness share a very high degree of overlap with those seen for the processing of facial trustworthiness (Bzdok et al., 2012; Mende-Siedlecki et al., 2012), suggesting that the same facial cues may influence multiple aspects of face processing and social

judgments. Oosterhof and Todorov (2008) argue that faces are assessed on two orthogonal dimensions, namely valence and dominance. Under this two dimensional analysis attractiveness aligns quite closely to the valence dimension, though attractiveness is also positively related to dominance. Yet attractiveness is more than valence since it is also affected by cues to health, sexual dimorphism, age, etc. Indeed, while O'Doherty et al. (2003) report that the orbitofrontal cortex is activated by both positive facial expressions and physical attractiveness, other brain systems responsive to beauty are unaffected by valence. Moreover most studies of brain responses to facial attractiveness use images that have neutral expressions and therefore limited in differences in valence.

A shortcoming of the current model of face perception (Figure 1) is that it does not explicitly define the invariant and variable aspects of faces beyond identity and emotion or movement, respectively, nor does it specify the temporal conditions of variant features. Skin color, for example, is a changeable aspect of facial appearance that influences a number of social judgments and can change over the course of several weeks with dietary changes (Whitehead et al., 2012), days with current health and blood perfusion changes (Stephen, Coetzee, Law Smith, & Perrett, 2009), or mere seconds with emotions and arousal (Hahn, Lefevre, & Perrett, 2013; Hahn, Whitehead, Albrecht, Lefevre, & Perrett, 2012; Levenson, 2003). Emotional expression and facial movements which the model (Haxby et al., 2000; Yovel & Belin, 2013) defines as variable aspects of the face again change over a very fast time course (and expressions and eye contact affect the attractiveness and rewarding nature of faces (Jones, Debruine, Little, Conway, & Feinberg, 2006; Kampe, Frith, Dolan, & Frith, 2001; O'Doherty et al., 2003). While these aspects undergo rapid variation,

identity, an invariant feature, is fixed across the lifespan. The morphological structure of the face is relatively unchanging (with the exception of facial growth during childhood an adolescence), but can be affected by variations in facial adiposity, and by skin texture changes. These physical aspects of facial appearance need to be defined within the model in order to gain a better understanding of the neural correlates of face perception and, in turn, the perception of facial attractiveness and other social cues.

IV. Sex differences and similarities in responses to attractiveness

Evolutionary theories of human mate preferences posit that physical attractiveness is a desirable trait in a potential mate in that it signals underlying quality, thus providing direct and indirect benefits to the individual. Both men and women rate physical attractiveness as an important characteristic in a potential mate, however a sex difference exists such that physical attractiveness is somewhat more important for men than it is for women when considering a potential mate (Buss & Barnes, 1986; Buss, 1989). This sex difference may arise because physical attractiveness can signal different aspects of "quality" in males and females. There is some evidence that the link between attractiveness and health is stronger in females than males (Hume & Montgomerie, 2001; Weeden & Sabini, 2005). Attractiveness of women is more closely related to young adult age than in men since fertility and fecundity are limited in women by menopause. Conversely, socioeconomic status during childhood is the best predictor of male physical attractiveness (Hume & Montgomerie, 2001). As such, physical attractiveness may be an indirect indicator of men's physiological quality, in addition to the direct benefits. Women place additional importance on traits not related to physical attractiveness such as social status (Buss & Schmitt, 1993). Cues to

current social status and resources during development may communicate information about men's resource provisioning abilities, thus influencing female preferences. When considering a potential mate, women must make trade-offs between genetic fitness indicators and indicators of the likely investment the male may make in the relationship as well as in future offspring (Gangestad & Simpson, 2000). Attractiveness preferences among women have been shown to vary with mating strategy – those women interested in short-term mating opportunities show increased preferences for physical attractiveness while those most interested in securing a long-term relationship show increased preferences for the man's earning potential (financial prospects) presumably to support a family (Buss & Schmitt, 1993). In light of these sex differences in the importance of physical attractiveness, sexual dimorphism may occur in the incentive salience of facial attractiveness.

Behavioral work utilizing the key-press paradigm has provided some evidence for sex differences in response to facial attractiveness. Both men and women will exert greater effort to view attractive than unattractive faces (Aharon et al., 2001; Dai, Brendl, & Ariely, 2010; Hahn, Xiao, Sprengelmeyer, & Perrett, 2013; Iaria et al., 2008; Levy et al., 2008) and there is some evidence that both sexes exert greater effort for opposite-sex faces than same-sex faces overall (Hahn, Xiao, et al., 2013; Iaria et al., 2008). Same-sex faces in general, however, may hold greater incentive salience among women than men (Dai et al., 2010; Hahn, Xiao, et al., 2013; Iaria et al., 2008; Levy et al., 2008), although attractiveness does impact on both the incentive salience of both same-sex and opposite-sex faces (e.g. Dai et al., 2010; Elman et al., 2005).

There is high agreement between the sexes on ratings of facial attractiveness, suggesting men and women perceive facial attractiveness similarly, but does the male brain and female brain respond the same way to attractive faces? Sex differences have been observed in some neural responses to facial attractiveness. For example, there is ERP evidence for a sex difference in the effect of facial attractiveness on the LPC component, with a larger effect in men than women (Oliver-Rodríguez et al., 1999; van Hooff et al., 2011). However, despite the evidence for sex differences in the processing of faces in general and the theoretical support for sexually dimorphic responses to attractiveness, men and women may process facial attractiveness similarly. This is true of the core and extended systems, including the processing of reward value of attractiveness within the NAcc and other ventral areas. Indeed, there is surprisingly limited evidence that this sex difference in the motivational aspect of attractiveness is mirrored in activation within the brain's reward circuitry. The only consistently reported sex difference appears to be in the higher order processing of reward related decisions that occurs in the OFC, where men have greater responses to facial attractiveness than do women. Using attractive and unattractive opposite-sex faces, Cloutier et al. (2008) found a sex difference in the OFC but not the NAcc or mPFC. Although Cloutier et al. (2008) did not find a sex difference in the cingulate response to facial attractiveness, Winston et al. (2007) observed a larger response for men than women in this region. Sexually dimorphic responses to facial attractiveness in the OFC may reflect underlying sex differences in the way in which men and women use information conveyed by attractiveness differently in mating related choices. Many studies have failed to find any evidence of a sex difference in responses to facial attractiveness (Chatterjee et al., 2009; Liang et al., 2010; O'Doherty et al., 2003; Vartanian et al., 2013). The apparent lack of sexual

dimorphism in response to facial attractiveness may be the result of faces being treated as a single stimulus category. When considering the sex of face presented, we begin to see evidence of potential sex differences. For opposite-sex faces, both men and women exhibit greater neural activity in response to attractive faces than unattractive faces (Kim et al., 2007), however men show a stronger effect in the prefrontal cortex than do women (mPFC: O'Doherty et al., 2003; OFC: Cloutier et al., 2008). For same-sex faces women, but not men, show increased activation of the NAcc in response to attractiveness (Kim et al., 2007).

Why are people motivated by attractiveness in same-sex faces? There are a number of evolutionarily driven explanations for this finding. Firstly, it may be that this behavior reflects the monitoring of competitors. Given that attractive people have high 'market value' (Hughes, Harrison, & Gallup Jr., 2004; Pawlowski & Dunbar, 1999; Michael Stirrat, Gumert, & Perrett, 2011), and are perceived as posing a greater threat to partner sexual fidelity (O'Connor & Feinberg, 2012), attractive individuals of either sex may be rivals for new mating opportunities or pose a threat to a current relationship. Alternatively motivations to view attractive individuals regardless of sex may reflect effort to identify valuable social partners (e.g., individuals who could act as friends/allies, who will cooperate, or who do not pose a disease threat). Exerting effort to view attractive individuals of either sex may also reflect a form of social comparison used to establish one's own market value, or social learning used to acquire fashion tips on how to improve one's market value. Notably, these are not mutually exclusive explanations; it may be that one or all of these factors drive motivation to view attractive individuals in addition to the mate-relevant aspects of facial attractiveness (i.e., sexual interest).

V. Babies on the brain: An infant face-specific neural response?

Due to the importance of parental care in the survival of human infants, the processing of infant faces may be somewhat distinct from that of adult faces. Infant facial morphology differs from that of adult faces, with the lower half of the face proportionately smaller in infant faces than it is in adult faces. Infants and young children have a characteristically short and wide face due to skeletal differences between infancy and adulthood; infants have a broad basicranial template, with an otherwise vertically short face because the nasal and mandibular regions are small due to their small body size and lesser pulmonary requirements (Bergersen, 1966; Enlow & Hans, 1996). These features typical of infants (i.e., large, bulbous forehead, large eyes, close-set features positioned low on the face, small chin, as well as some body features such as short limbs and chubbiness) form the 'baby schema'. Lorenz proposed the *Kindchenschema* as an innate releasing mechanism for care-taking behavior, affective orientation toward infants, and decreased aggression, which is triggered by infant's morphological and behavioural features (Lorenz, 1943). Note that these stereotypical visual features form the baby schema, whereas Lorenz's *Kindchenschema* refers to the caretaking mechanism triggered by the baby schema, which includes both sensory and behavioral infant characteristics.

Behavioral studies have demonstrated that humans are drawn to this baby schema; infant faces are attentionally prioritized above adult faces and other social stimuli (Brosch, Sander, & Scherer, 2007; Hodsoll, Quinn, & Hodsoll, 2010; Proverbio, 2011). Preferences for the baby schema are evident in young children as well as adults (Sanefuji, Ohgami, & Hashiya, 2007). These preferences extend across species

(Archer & Monton, 2011; Lehmann, Huis in't Veld, & Vingerhoets, 2013; Little, 2012; Lorenz, 1943) and have been observed for inanimate objects such as cars and toys (Hinde & Barde, 1985; Miesler, Leder, & Herrmann, 2011). Some work even suggests that face processing limitations, such as the other-race effect, may not affect infant faces (Proverbio, 2011; but see Hodsoll et al., 2010).

A number of recent studies have explored the neural basis of processing differences for infant and adult faces. This neuroimaging work has provided evidence of an infant-specific neural response. Both ERP and fMRI work has suggested that infant faces may be perceived more rapidly than adult faces. Early structural encoding responses are larger for infant faces than adult faces (Proverbio et al., 2010b; Proverbio, Riva, Zani, & Martin, 2011); source localization techniques suggest that these differences may originate in the FG, cingulate, and OFC. There is some evidence for the OFC as a source of the infant-specific neural response. Using MEG, Kringelbach et al. (2008) observed early activity at approximately 140ms in response to infant faces but not adult faces in the OFC. This infant-specific OFC response is diminished when viewing infants suffering from facial anomalies, such as cleft lip, that disrupt the baby schema (Parsons et al., 2013). Viewing both adult and infant faces elicited similar activation patterns, initiated in the posterior visual cortex and spreading along both ventral and dorsal visual pathways. An enhanced infant face-response was observed initially in the OFC at 130ms after face presentation, whereas responses in the FFA were similar in magnitude for adult and infant faces until 160ms after presentation. Kringelbach et al. suggest that this result indicates the OFC may provide a top-down amplification of the activity in the FFA specifically related to

infant faces and is evidence of a specific and rapid neural signature for the parental instinct, evident in both parous and nulliparous individuals.

The role of Haxby's core system in the preferential processing of infant faces is currently unclear. Kringelbach et al. (2008) did not find any evidence of a baby-specific response in the neural regions of the core system, however other studies have indicated that viewing infant faces correlates with increased activation in the FG and IFG (Bartels & Zeki, 2004; Caria et al., 2012; Glocker et al., 2009; Noriuchi, Kikuchi, & Senoo, 2008; Ranote et al., 2004; Strathearn, Li, Fonagy, & Montague, 2008; Swain, 2008). Methodological differences, as well as differences in the imaging technique used, may contribute to this discrepancy; many studies investigating neural responses to infant faces are conducted on parous populations, while others are conducted using nulliparous samples.

Parental status may modulate neural (Seifritz et al., 2003) and behavioral (Lehmann et al., 2013) responses to infants. ERP evidence demonstrates that neural responses to infant faces are smaller in nulliparous individuals than parous individuals (Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006; Weisman, Feldman, & Goldstein, 2012), and that nulliparous women may exhibit a more right-lateralized response, similar to that seen in men, to infant faces than parous women (Proverbio et al., 2006). Within parous individuals, responses appear to be stronger to stimuli depicting own-infant compared to unfamiliar infants. Although this pattern has been observed in the core system (Lenzi et al., 2009; Noriuchi et al., 2008), it is especially true of responses in the extended system, including the brain's reward circuitry (Nitschke et al., 2004; Noriuchi et al., 2008; Ranote et al., 2004; Strathearn et al., 2008; Swain,

Lorberbaum, Kose, & Strathearn, 2007; Wittfoth-Schardt et al., 2012). Increased activation in response to own- versus unfamiliar-infants has been observed in the OFC, PFC, insula, cingulate, putamen, VTA, as well as the NAcc and ventral striatum. Some researchers have proposed that activation of core system neural components, such as the IFG and STS, may relate to empathizing with the infant, thus reflecting activation of the mirror neuron system, rather than face processing differences, specifically (Kuo, Carp, Light, & Grewen, 2012; Lenzi et al., 2009).

Evidence that the extended system exhibits a baby-specific response comes from studies of both parous and nulliparous individuals, as well as animal models of parental behavior (Lavi-Avnon et al., 2008; Michael Numan, 2007). In mice, the display of parental behavior has been observed to be unaffected by lesions in the neocortex provided the septum is spared (Carlson & Thomas, 1968). Similarly, in rats infant-related cues trigger dopamine release in reward related structures such as the NAcc (Champagne et al., 2004) and maternal behavior is disrupted following lesions along mesocorticolimbic pathways (Hansen, 1994; Numan & Numan, 1997). Similarly, reward circuitry in humans has been associated with parental attachment (Glocker et al., 2009; Kringelbach et al., 2008; Ranote et al., 2004; Swain et al., 2007). In studies using parous samples, neural activation in response to infant faces has been observed in the thalamus and cingulate (Bartels & Zeki, 2004), the ventral striatum, including the NAcc (Bartels & Zeki, 2004; Mascaro, Hackett, & Rilling, 2013; Ranote et al., 2004; Strathearn, Fonagy, Amico, & Montague, 2009; Strathearn et al., 2008; Swain, 2008) and OFC (Bartels & Zeki, 2004; Nitschke et al., 2004). Similarly, in samples of exclusively nulliparous individuals, neural activation in response to infant faces has been observed in the thalamus and cingulate (Caria et al.,

2012; Glocker et al., 2009), the ventral striatum, including the NAcc, (Glocker et al., 2009), and the OFC (Glocker et al., 2009). Overall, in light of the consistently observed activation of reward-related brain regions, there is strong evidence that infant faces may hold particularly strong incentive salience.

VI. Sexually dimorphic responses to infants

Although the baby-specific neural response has been observed in both men and women, there is some evidence that it may be a sexually dimorphic response. The baby schema effect on early indices of visual processing is stronger in women than men (Proverbio et al., 2006, 2010b, 2011), although one study observed this sex difference in parous, but not nulliparous, individuals (Proverbio et al., 2006). Source localization of these ERP components implicates the FG, hippocampus, thalamus, cingulate, and the OFC, and fMRI studies have confirmed that components of both Haxby's core system and the so-called extended system show sex differences with respect to the magnitude of the baby-specific response (Glocker et al., 2009; Seifritz et al., 2003).

These sex differences in neural responses to infant stimuli are also evident in behavioral measures of the incentive salience of infants. A number of studies utilizing the effort-based key-press task described previously have shown that infant faces hold greater incentive salience for women than they do for men. This has been shown when infant faces were provided as viewing options along with same-sex and opposite-sex adult faces (Hahn et al., 2013; but see Parsons, Young, Kumari, Stein, & Kringelbach, 2011) as well as when animal faces were used as additional viewing options (Charles, Alexander, & Saenz, 2013). Similarly, infant faces have been shown

to capture women's attention to a greater extent that same-sex or opposite-sex faces, whereas infant faces capture men's attention more so than same-sex faces, but much less than opposite-sex faces (Cárdenas, Harris, & Becker, 2013; but see Brosch et al., 2007).

VII. Infant cuteness

Physical attractiveness may also influence neural and behavioral responses to infant faces. Many studies have demonstrated that this baby schema (i.e., large, bulbous forehead, large eyes, close-set features positioned low on the face, small chin) is directly related to perceptions of cuteness or attractiveness (Alley, 1981; Boukydis, 1981; Brooks & Hochberg, 1960; Glocker et al., 2008; Hildebrandt & Fitzgerald, 1979; Hildebrandt, 1978; Lehmann et al., 2013; Little, 2012; Sternglanz, Gray, & Murakami, 1977). According to Lorenz's (1943) *Kindchenschma,* cuter infants would receive more care and positive interaction, as well as experience decreased aggression. These behavioral outcomes would have obvious advantages for infant survival rates among species with high levels parental care, such as humans. Indeed, infant attractiveness or cuteness is linked to positive affective responses (Hildebrandt, 1978; Langlois, Ritter, Casey, & Sawin, 1995; Power, Hildebrandt, & Fitzgerald, 1982; Stephan & Langlois, 1984), motivation to care for the infant (Alley, 1983; Badr & Abdallah, 2001; Glocker et al., 2008; Maier, Holmes, Slaymaker, & Reich, 1984; Volk, Lukjanczuk, & Quinsey, 2005; Volk & Quinsey, 2002; Waller, Volk, & Quinsey, 2004; Weiss, 1994), and reduction in negative affective responses to infants (Frodi, 1978; Langlois et al., 1995). Exposure to cute infants and young animals has also been shown to stimulate increased carefulness or tenderness (Nittono, Fukushima, Yano, & Moriya, 2012; Sherman, Haidt, & Coan, 2009).

Importantly, infant cuteness may be indicative of underlying health or viability. Infants suffering from low birth weight or other health defects are perceived as less cute (Volk, Lukjanczuk, & Quinsey, 2005; Waller, Volk, & Quinsey, 2004), and in normal infants perceptual ratings of cuteness have been found to correlate with perceptual ratings of health (Volk & Quinsey, 2002). The link between baby schema and perceptions of cuteness extends to the age of about 4.5 years (Luo, Lee, & Li, 2011), which may reflect a decreased reliance on parental care with age. The link between cuteness, health, and caretaking motivation may serve an adaptive function – that is, to optimize allocation of parental resources according to perceived offspring quality or viability as a sick infant simultaneously increases the cost of parental investment and decreases the chances of investment payoff. Although all infants stimulate caretaking responses, there is evidence that cuteness can stimulate disproportionate affection.

To date, only one study has explored the modulatory effects of cuteness on neural responses to infant faces. Glocker et al. (2009) found that experimentally manipulating the level of baby schema within individual infant faces directly affected activation in the cingulate cortex, precuneus, left FG, and the NAcc. In each of these regions, greater activation was observed for faces with high baby schema compared to unmanipulated faces or those with low baby schema. The impact of baby schema, or cuteness, on activation within the extended system could directly impact caregiver behavior. For example, modulation of the NAcc response could affect approach-avoidance behavior, impacting upon urges to interact with the infant and engage in physical contact, which may positively feedback to enhance the mother-infant bond.

Similarly, modulation of activation in attentional systems, including areas such as the precuneus (Le, Pardo, & Hu, 1998) may influence the attention-capturing effects of the baby schema.

VII. Sexual dimorphisms in responses to infant cuteness

Although sexual dimorphisms in the modulation of neural responses by infant cuteness have yet to be explored, there is behavioral evidence that these sexual dimorphisms exist. They have been observed in sensitivity to the baby schema, with women typically showing greater perceptual discrimination than men for faces that have been subtly manipulated along the baby schema (Berman, 1980; Fullard & Reiling, 2013; Glocker et al., 2008; Hildebrandt, 1978; Maestripieri & Pelka, 2002; Sprengelmeyer et al., 2009). Using computer graphic techniques to subtly manipulate the baby schema, thereby increasing or decreasing cuteness within an individual infant face, two studies have found that women outperform men in terms of ability to detect changes to the baby schema, suggesting that women may be more sensitive to infant facial cues (Lobmaier, Sprengelmeyer, Wiffen, & Perrett, 2010; Sprengelmeyer et al., 2009). Importantly, these sex differences were not observed for sensitivity to face cues of infant age or emotion (Lobmaier et al., 2010). In addition to this sex difference in discrimination, women also tend to rate infants as cuter than men do, overall (Lehmann et al., 2013; Parsons, Young, Kumari, et al., 2011). Additionally, there may be a hormonal link to sensitivity to infant cuteness; Sprengelmeyer et al. (2009) observed increased perceptual discrimination in pre-menopausal compared to post-menopausal women, as well as in pre-menopausal women using hormonal contraceptives (which artificially elevate estrogen and progestogens) compared to pre-menopausal naturally cycling women.

Infant cuteness also influences a number of behavioral outcomes differently among men and women. For example, the baby schema can elicit stronger urges to protect children in women than in men (Alley, 1983), and stronger caretaking motivation in women than in men (Glocker et al., 2008). The observed sex differences in caretaking motivation due to infant cuteness would suggest that the motivational value, or incentive salience, of infant cuteness is also sexually dimorphic. Indeed, cuteness has been shown to strongly predict the motivation to view infant stimuli (Sprengelmeyer, Lewis, Hahn, & Perrett, 2013). There is mixed evidence, however, as to whether or not sex differences exist in the incentive salience of infant cuteness. Using a set of infant faces that had been manipulated to appear more or less cute (i.e., high vs low baby schema), Hahn et al., (2013) found that both men and women exert differential effort based on infant cuteness. Conversely, Parsons et al. (2011) did not find any evidence for sex differences in the incentive salience of infant faces with low, average, or high baby schema. When using infant faces with deformities, such as cleft palate, Yamamoto et al. (2009) found that women spent significantly less time viewing abnormal infants than men did, suggesting these faces may be more aversive to women (but see Parsons, Young, Parsons, et al., 2011). To date, these key-pressing studies have not explored effects of parental status on the incentive salience of infants.

Importantly, there may also be hormonal correlates of interest in infants. Oxytocin, prolactin, and vasopressin have long been known to influence parental responsiveness (Delahunty, McKay, Noseworthy, & Storey, 2007; Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010; A S Fleming, Ruble, Krieger, & Wong, 1997;

Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010; Storey, Walsh, Quinton, & Wynne-Edwards, 2000). Similarly, estrogen has been shown to be linked to maternal drive in female primates, including humans (Law Smith et al., 2012; Ramirez, Bardi, French, & Brent, 2004). Recent work has also suggested men and women with children have lower testosterone than those without (Gettler, McDade, Feranil, & Kuzawa, 2011; Kuzawa, Gettler, Huang, & McDade, 2010), and an inverse relationship between testosterone and paternal caregiving behaviors among fathers (Fleming, Corter, Stallings, & Steiner, 2002; Gettler et al., 2011; Mascaro et al., 2013). A recent model proposed by van Anders et al. (2001, the Steroid/Peptide Model) purports that testosterone regulates both nurturant and protective responses to infants (van Anders, Goldey, & Kuo, 2011). Hahn and colleagues recently (2014) proposed and additional role of testosterone in modulating differential responses to infant cuteness, given their evidence that women's endogenous testosterone levels are linked to the reward value of infant cuteness. Neural responses to infant stimuli, both visual and auditory, have also been linked to testosterone levels, particularly in the caudate (Kuo et al., 2012) and thalamocingulate circuit (Bos, Hermans, Montoya, Ramsey, & van Honk, 2010), respectively. Future work may provide a better understanding of the links between hormones, neural responses, and behavioral responses to infant-related stimuli.

Overall, there is converging evidence for heightened processing of the baby schema within components of the dopaminergic motivational system, as well as some aspects of Haxby's core face processing system. These results suggest there may be increased attention to infant as compared to adult faces or other social stimuli. Additionally, these general responses to infants appear to be stronger in parents than non-parents

and stronger in women than in men, however individual differences in responses to infant faces have yet to be explored. Sex differences are apparent in a number of behavioral responses to infant cuteness, and future neuroimaging work may illuminate the neural correlates of such sex differences.

VIII. Conclusions

Facial perception, and the perception of attractiveness, relies on a distributed cortical network involving both visual and reward systems. Neuroimaging work has provided converging evidence for sex differences in general face perception, especially with regards to the lateralization of neural responses to facial stimuli. Although evolutionary theories of mate preferences would support the notion of sex differences in neural responses to facial attractiveness, there is surprisingly little evidence for such sex differences in the imaging work reviewed here. Any differences are potentially complicated by differences in the sexual orientation of men and women with respect to the stimuli; hence, there is a need to consider same-sex and opposite-sex faces separately. While it is commonly posited that attractiveness in a potential mate matters more to men than it does to women, physical attractiveness, and especially facial attractiveness, is an important characteristic for both men and women when assessing potential mates and potential rivals. Perhaps it is unsurprising then that both men and women exhibit increased neural activation in the dopaminergic motivational system when viewing attractive as compared to unattractive faces.

Indeed, attractive facial stimuli are powerful motivators, yet the neural basis of attractiveness not been studied extensively. Here, we have reviewed behavioral and neural responses to *both* adult and infant faces. These may seem disparate topics, yet

both are powerful motivational stimuli. Furthermore there is evidence emerging that sexual interest in adult men and desire for infants are linked in heterosexual women (Batres et al., 2014). Hence a unified reproductive drive, perhaps mediated by sex steroid hormones, could be affecting the response of the dopaminergic reward systems to both attractive faces and cute infant facial features.

Acknowledgements

Amanda Hahn is funded by European Research Council Grant 282655.

Figures & Captions

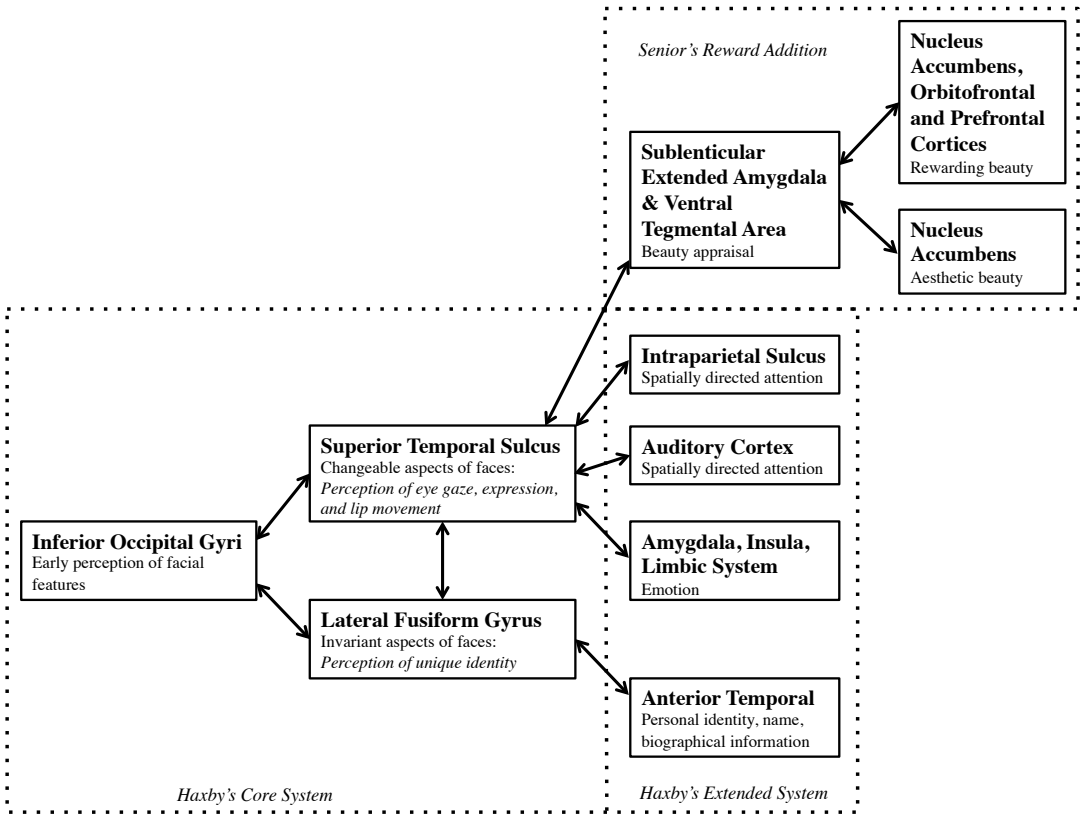

Figure 1. The distributed neural network for face processing as described by Haxby et al. (2000) and Senior (2003).

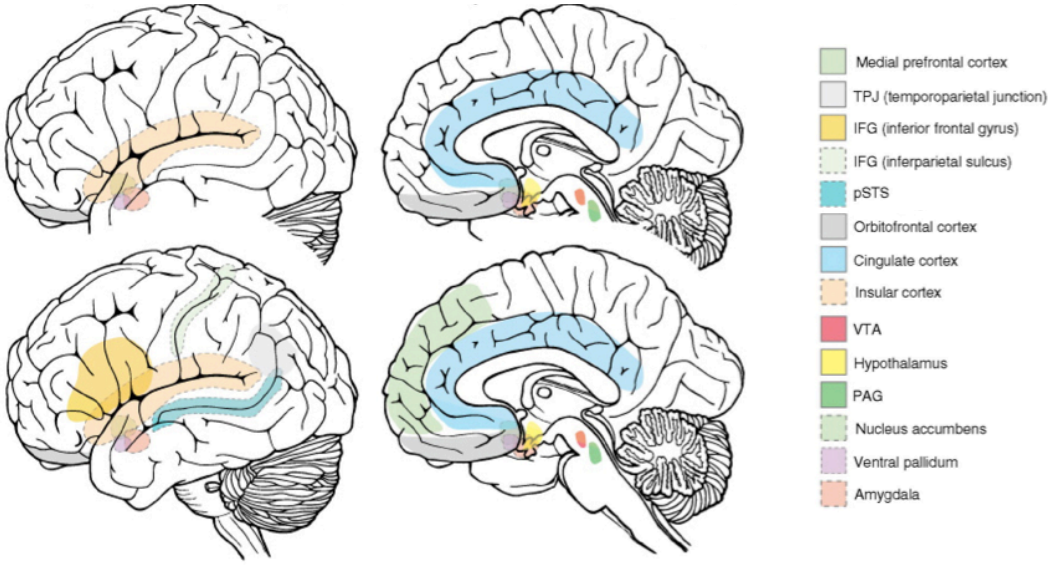

Figure 2. Schematic figure depicting the approximate anatomical locations of the brain regions involved in face processing (both physical attractiveness and faces more generally). Image courtesy of Parsons et al. (2010), Progress in Neurobiology.

References

Abramov, I., Gordon, J., Feldman, O., & Chavarga, A. (2012). Sex and vision II: color appearance of monochromatic lights. *Biology of sex differences*, *3*(1), 21. doi:10.1186/2042-6410-3-21

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, *32*(3), 537–551. doi:10.1016/S0896-6273(01)00491-3

Alley, T. R. (1981). Head Shape and the Perception of Cuteness. *Developmental Psychology*, *17*(5), 650–654.

Alley, T. R. (1983). Infantile head shape as an elicitor of adult protection. *Journal of Developmental Psychology*, *29*(4), 411–427.

Amrhein, C., Mühlberger, A., Pauli, P., & Wiedemann, G. (2004). Modulation of event-related brain potentials during affective picture processing: a complement to startle reflex and skin conductance response? *International journal of psychophysiology*, *54*(3), 231–40. doi:10.1016/j.ijpsycho.2004.05.009

Archer, J., & Monton, S. (2011). Preferences for Infant Facial Features in Pet Dogs and Cats. *Ethology*, *117*(3), 217–226. doi:10.1111/j.1439-0310.2010.01863.x

Aron, A., Fisher, H., Mashek, D. J., Strong, G., Li, H., Brown, L. L., & Reward, L. L. B. (2005). Reward, motivation, and emotion systems associated with early-stage intense romantic love. *Journal of neurophysiology*, *94*(1), 327–37. doi:10.1152/jn.00838.2004

Badr, L. K., & Abdallah, B. (2001). Physical attractiveness of premature infants affects outcome at discharge from the NICU. *Infant Behavior and Development*, *24*(1), 129–133. doi:10.1016/S0163-6383(01)00068-6

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, *21*(3), 1155–66. doi:10.1016/j.neuroimage.2003.11.003\

Batres, C., Jones, B.C., Feinberg, D.R., DeBruine, L.M. & Perrett, D.I. (2014, March). *Ideal family size and variation in sexual orientation amongst heterosexual women predict preferences for male facial masculinity.* Poster presented at the annual meeting of the European Human Behavior and Evolution Association (EHBEA), Bristol, UK.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.

Bergersen, E. O. (1966). The directions of facial growth from infancy to adulthood. *Facial Growth*, *36*(1), 18–43.

Berman, P. W. (1980). Are women more responsive than men to the young? A review of developmental and situational variables. *Psychological Bulletin*, *88*(3), 668–695.

Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, *26*(9), 507–513. doi:10.1016/S0166-2236(03)00233-9

Berscheid, E., & Walster, E. (1974). Physical attractiveness. *Advances in Experimental Social Psychology*, *7*, 157–215.

Bilalic, M., Langner, R., Ulrich, R., & Wolfgang, G. (2011). Many faces of expertise: Fusiform face area in chess experts and novices. *The Journal of Neuroscience, 31,* 10206-10214.

Bishop, K. M., & Wahlsten, D. (1997). Sex differences in the human corpus callosum: myth or reality? *Neuroscience and biobehavioral reviews*, *21*(5), 581–601. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9353793

Bloch G. L., Gorski R. A. (1988). Estrogen/progesterone treatment in adulthood affects the size of several components of the medial preoptic area in the male rat. J Comp Neurol, 275: 613-22.

Boukydis, C. F. (1981). Adult perception of infant appearance: a review. *Child psychiatry and human development*, *11*(4), 241–54. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7249803

Bray, S., & O'Doherty, J. (2007). Neural coding of reward-prediction error signals during classical conditioning with attractive faces. *Journal of neurophysiology*, *97*(4), 3036–45. doi:10.1152/jn.01211.2006

Brooks, V., & Hochberg, J. (1960). A psychophysical study of "cuteness." *Perceptual and Motor Skills*, *11*, 205.

Brosch, T., Sander, D., & Scherer, K. R. (2007). That baby caught my eye... attention capture by infant faces. *Emotion*, *7*(3), 685–9. doi:10.1037/1528-3542.7.3.685

Bruce, V., & Young, A. (1986). Understanding face recognition. *British journal of psychology (London, England : 1953)*, *77 (Pt 3)*, 305–27. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3756376

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1–49. doi:10.1017/S0140525X00023992

Buss, D. M., & Barnes, M. (1986). Preferences in human mate selection. *Journal of Personality and Social Psychology*, *50*(3), 559–570. doi:10.1037//0022-3514.50.3.559

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*(2), 204–232.

Bzdok, D., Langner, R., Caspers, S., Kurth, F., Habel, U., Zilles, K., … Eickhoff, S. B. (2011). ALE meta-analysis on facial judgments of trustworthiness and attractiveness. *Brain structure & function*, *215*(3-4), 209–23. doi:10.1007/s00429-010-0287-4

Bzdok, D., Langner, R., Hoffstaedter, F., Turetsky, B. I., Zilles, K., & Eickhoff, S. B. (2012). The modular neuroarchitecture of social judgements on faces. *Cerebral Cortex, 22*, 951-961.

Bzdok, D., Langner, R., Schilbach, L., Engemann, D. A., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2013). Segregation of the human medial prefrontal cortex in social cognition. *Frontiers in Human Neuroscience, 7*, 232.

Cárdenas, R. A., Harris, L. J., & Becker, M. W. (2013). Sex differences in visual attention toward infant faces. *Evolution and Human Behavior*, *34*(4), 280–287. doi:10.1016/j.evolhumbehav.2013.04.001

Caria, A., Falco, S. De, Venuti, P., Lee, S., Esposito, G., Rigo, P., … Bornstein, M. H. (2012). Species-specific response to human infant faces in the premotor cortex. *NeuroImage*, *60*(2), 884–93. doi:10.1016/j.neuroimage.2011.12.068

Carlson, N. R., & Thomas, G. J. (1968). Maternal behavior of mice with limbic lesions. *Journal of Comparative and Physiological Psychology*, *66*, 731–737. doi:10.1037/h0026513

Champagne, F. A., Chretien, P., Stevenson, C. W., Zhang, T. Y., Gratton, A., & Meaney, M. J. (2004). Variations in nucleus accumbens dopamine associated with individual differences in maternal behavior in the rat. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *24*(17), 4113–23. doi:10.1523/JNEUROSCI.5322-03.2004

Charles, N. E., Alexander, G. M., & Saenz, J. (2013). Motivational value and salience of images of infants. *Evolution and Human Behavior*. doi:10.1016/j.evolhumbehav.2013.06.005

Chatterjee, A., Thomas, A., Smith, S. E., & Aguirre, G. K. (2009). The neural response to facial attractiveness. *Neuropsychology*, *23*(2), 135–43. doi:10.1037/a0014430

Chen, W., Liu, C. H., & Nakabayashi, K. (2012). Beauty hinders attention switch in change detection: the role of facial attractiveness and distinctiveness. *PloS one*, *7*(2), e32897. doi:10.1371/journal.pone.0032897

Cloutier, J., Heatherton, T. F., Whalen, P. J., & Kelley, W. M. (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial

attractiveness. *Journal of Cognitive Neuroscience*, *20*(6), 941–951. doi:10.1162/jocn.2008.20062

Coetzee, V., Perrett, D. I., & Stephen, I. D. (2009). Facial adiposity: A cue to health? *Perception*, *38*(11), 1700–1711. doi:10.1068/p6423

Croxson, P. L., Johansen-Berg, H., Behrens, T. E., Robson, M. D., Pinsk, M. A., Gross, C. G., Richter, W., Richter, M. C., Kastner, S., & Rushworth, M. F. (2005). Quantitative investigation of connections of the prefrontal cortex in the human and macaque using probabilistic diffusion tractography. *Journal of Neuroscience, 25*, 8854-8866.

Dai, X., Brendl, C. M., & Ariely, D. (2010). Wanting, liking, and preference construction. *Emotion*, *10*(3), 324–34. doi:10.1037/a0017987

Deffke, I., Sander, T., Heidenreich, J., Sommer, W., Curio, G., Trahms, L., & Lueschow, A. (2007). MEG/EEG sources of the 170-ms response to faces are co-localized in the fusiform gyrus. *NeuroImage*, *35*(4), 1495–501. doi:10.1016/j.neuroimage.2007.01.034

Delahunty, K. M., McKay, D. W., Noseworthy, D. E., & Storey, A. E. (2007). Prolactin responses to infant cues in men and women: effects of parental experience and recent infant contact. *Hormones and behavior*, *51*(2), 213–20. doi:10.1016/j.yhbeh.2006.10.004

Dion, K. K., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology*, *24*, 285–290.

Elman, I., Ariely, D., Mazar, N., Aharon, I., Lasko, N. B., Macklin, M. L., … Pitman, R. K. (2005). Probing reward function in post-traumatic stress disorder with beautiful facial images. *Psychiatry research*, *135*(3), 179–83. doi:10.1016/j.psychres.2005.04.002

Enlow, D. H., & Hans, M. G. (1996). *Essentials of Facial Growth*. Philadelphia, PA: W.B. Saunders Company.

Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. *Cerebral cortex (New York, N.Y. : 1991)*, *17*(10), 2400–6. doi:10.1093/cercor/bhl148

Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., & Zagoory-Sharon, O. (2010). Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. *Psychoneuroendocrinology*, *35*(8), 1133–41. doi:10.1016/j.psyneuen.2010.01.013

Fink, B., Grammer, K., & Thornhill, R. (2001). Human (Homo sapiens) facial attractiveness in relation to skin texture and color. *Journal of Cognitive Psychology*, *115*(1), 92–99. doi:10.1037/0735-7036.115.1.92

Fisher, H., Sandblom, J. Herlitz, A., Fransson, P., Wright, C. I., & Backman, L. (2004). Sex-differential brain activation during exposure to female and male faces. *NeuroReport, 15*, 235-238.

Fleming, A S, Ruble, D., Krieger, H., & Wong, P. Y. (1997). Hormonal and experiential correlates of maternal responsiveness during pregnancy and the

puerperium in human mothers. *Hormones and behavior*, *31*(2), 145–58. doi:10.1006/hbeh.1997.1376

Fleming, Alison S., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and Prolactin Are Associated with Emotional Responses to Infant Cries in New Fathers. *Hormones and Behavior*, *42*(4), 399–413. doi:10.1006/hbeh.2002.1840

Freiwald, W. A., & Tsao, D. Y. (2010). Functional Compartmentalization and Viewpoint Generalization Within the Macaque Face-Processing System. *Science*, *330*(6005), 845–851. doi:10.1126/science.1194908.Functional

Frodi, A. M. (1978). Fathers' and mothers' responses to the faces and cries of normal and premature infants. *Developmental Psychology*, *14*(5), 490–498. doi:10.1037//0012-1649.14.5.490

Fullard, W., & Reiling, A. M. (2013). An Investigation of Lorenz ' s " Babyness ", *47*(4), 1191–1193.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*(4), 573–587. doi:10.1017/S0140525X0000337X

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature neuroscience*, *2*(6), 568–73. doi:10.1038/9224

Gettler, L. T., McDade, T. W., Feranil, A. B., & Kuzawa, C. W. (2011). Longitudinal evidence that fatherhood decreases testosterone in human males. *Proceedings of*

the National Academy of Sciences, *108*(39), 16194–16199. doi:10.1073/pnas.1105403108

Glocker, M. L., Langleben, D. D., Ruparel, K., Loughead, J. W., Gur, R. C., & Sachser, N. (2008). Baby schema in infant faces induces cuteness perception and motivation for caretaking in adults. *Ethology*, *115*(3), 257–263. doi:10.1111/j.1439-0310.2008.01603.x

Glocker, M. L., Langleben, D. D., Ruparel, K., Loughead, J. W., Valdez, J. N., Griffin, M. D., … Gur, R. C. (2009). Baby schema modulates the brain reward system in nulliparous women. *Proceedings of the National Academy of Sciences*, *106*(22), 9115–9119. doi:10.1073/pnas.0811620106

Goldstein, J. M., Seidman, L. J., Horton, N. J., Makris, N., Kennedy, D. N., Caviness, V. S., … Tsuang, M. T. (2001). Normal sexual dimorphism of the adult human brain assessed by in vivo magnetic resonance imaging. *Cerebral cortex (New York, N.Y. : 1991)*, *11*(6), 490–7. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11375910

Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010). Oxytocin and the development of parenting in humans. *Biological psychiatry*, *68*(4), 377–82. doi:10.1016/j.biopsych.2010.02.005

Gray, A. W., & Boothroyd, L. G. (2012). Female facial appearance and health. *Evolutionary Psychology*, *10*(1), 66–77.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature neuroscience*, *7*(5), 555–62. doi:10.1038/nn1224

Hahn, A. C., Fisher, C. I., DeBruine, L. M., & Jones, B. C. (2014, August). *Women's testosterone upregulates the reward value of baby schema.* Talk presented at the annual Human Behavior and Evolution Society (HBES) conference. Natal, Brazil.

Hahn, A. C., Lefevre, C. E., & Perrett, D. I. (2013). What does sexual arousal look like? Temperature and color changes in the face. In *European Human Behaviour & Evolotion Association*. Amsterdam. Retrieved from http://www.ehbea2013.com/ehbea_details/upload/files/1534.pdf

Hahn, A. C., Whitehead, R. D., Albrecht, M., Lefevre, C. E., & Perrett, D. I. (2012). Hot or not? Thermal reactions to social contact. *Biology letters*, *8*(5), 864–7. doi:10.1098/rsbl.2012.0338

Hahn, A. C., Xiao, D., Sprengelmeyer, R., & Perrett, D. I. (2013). Gender differences in the incentive salience of adult and infant faces. *Quarterly journal of experimental psychology (2006)*, *66*(1), 200–8. doi:10.1080/17470218.2012.705860

Halgren, E., Dale, a M., Sereno, M. I., Tootell, R. B., Marinkovic, K., & Rosen, B. R. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human brain mapping*, *7*(1), 29–37. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9882088

Halgren, E., Raij, T., Marinkovic, K., Jousmäki, V., & Hari, R. (2000). Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral cortex (New York, N.Y. : 1991)*, *10*(1), 69–81. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10639397

Halit, H., Haan, C. A. M. De, & Johnson, M. H. (2000). Modulation of event-related potentials by prototypical and atypical faces, *11*(9), 1871–1875.

Hamann, S. (2005). Sex differences in the responses of the human amygdala. The Neuroscientist : a review journal bringing neurobiology, neurology and psychiatry, 11(4), 288–93. doi:10.1177/1073858404271981

Hamermesh, D. S., & Biddle, J. E. (1994). Beauty and the labor market. *The American Economic Review*, *84*(5), 1174–1194.

Hampshire, A., Chaudhry, A. M., Owen, A. M., & Roberts, A. C. (2012). Dissociable roles for lateral orbitofrontal cortex and lateral prefrontal cortex during preference driven reversal learning. *NeuroImage*, *59*(4), 4102–12. doi:10.1016/j.neuroimage.2011.10.072

Hansen, S. (1994). Maternal behavior of female rats with 6-OHDA lesions in the ventral striatum: characterization of the pup retrieval deficit. *Physiology & behavior*, *55*(4), 615–20. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8190785

Haxby, J. V, Hoffman, E. a, & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological psychiatry*, *51*(1), 59–67. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11801231

Haxby, J. V, Hoffman, E., & Gobbini, M. (2000). The distributed human neural system for face perception. *Trends in cognitive sciences*, *4*(6), 223–233. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10827445

Henderson, J. J., & Anglin, J. M. (2003). Facial attractiveness predicts longevity. *Evolution and Human Behavior*, *24*(5), 351–356. doi:10.1016/S1090-5138(03)00036-9

Hildebrandt, K. A. (1978). Adults' responses to infants varying in perceived cuteness. *Behavioural Processes*, *3*, 159–172.

Hildebrandt, K. A., & Fitzgerald, H. E. (1979). Facial feature determinants of perceived infant attractiveness. *Infant Behavior and Development*, *2*, 329–339. doi:10.1016/S0163-6383(79)80043-0

Hinde, R. A., & Barde, L. A. (1985). The evolution of the teddy bear. *Animal Behaviour*, *33*(4), 1371–1373.

Hodsoll, J., Quinn, K. a, & Hodsoll, S. (2010). Attentional prioritization of infant faces is limited to own-race infants. *PloS one*, *5*(9), 1–5. doi:10.1371/journal.pone.0012509

Hosoda, M., Stone-Romero, E. F., & Coats, G. (2003). The effects of physical attractiveness on job-related outcomes: A meta-analysis of experimental studies. *Personnel Psychology*, *56*, 431–462.

Hughes, S. M., Harrison, M. A., & Gallup Jr., G. G. (2004). Sex differences in mating strategies: Mate guarding, infidelity and multiple concurrent sex partners.

Sexualities, Evolution & Gender, *6*(1), 3–13. doi:10.1080/14616660430001733588

Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of "quality" in women and men. *Evolution and Human Behavior*, *22*(2), 93–112.

Hyde, J. S. & Linn, M. C. (1988). Gender differences in verbal ability: A meta-analysis. *Psychological Bulletin*, 104(1), 53-69.

Iaria, G., Fox, C. J., Waite, C. T., Aharon, I., & Barton, J. J. S. (2008). The contribution of the fusiform gyrus and sperior temporal sulcus in processing facial attractiveness: Neuropsychological and neuroimaging evidence. *Neuroscience*, *155*(2), 409–422. doi:10.1016/j.neuroscience.2008.05.046.The

Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. *International Jounal of Psychophysiology*, *63*(2), 181–5. doi:10.1016/j.ijpsycho.2006.03.010

Ishizu, T, & Zeki, S. (2013). The brain's specialized systems for aesthetic and perceptual judgment. *The European journal of neuroscience*, *37*(9), 1413–20. doi:10.1111/ejn.12135

Ishizu, Tomohiro, & Zeki, S. (2011). Toward a brain-based theory of beauty. *PloS one*, *6*(7), e21852. doi:10.1371/journal.pone.0021852

Itier, Roxane J, Herdman, A. T., George, N., Cheyne, D., & Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain research*, *1115*(1), 108–20. doi:10.1016/j.brainres.2006.07.072

Itier, Roxanne J, & Taylor, M. J. (2004). Source analysis of the N170 to faces and objects. *NeuroReport*, *15*, 1261–1265.

Jacobsen, T., Schubotz, R. I., Höfel, L., & Cramon, D. Y. V. (2006). Brain correlates of aesthetic judgment of beauty. *NeuroImage*, *29*(1), 276–85. doi:10.1016/j.neuroimage.2005.07.010

Johnson BW, McKenzie KJ, Hamm JP (2002) Cerebral asymmetry for mental rotation: effects of response hand, handedness and gender. Neuroreport 13: 1929–1932.

Johnston, V. S., & Oliver-Rodríguez, J. C. (1997). Facial beauty and the late positive component of event-related potentials. *The Journal of Sex Research*, *34*(2), 188–198.

Jokela, M. (2009). Physical attractiveness and reproductive success in humans: Evidence from the late 20 century United States. *Evolution and Human Behavior*, *30*(5), 342–350. doi:10.1016/j.evolhumbehav.2009.03.006

Jones, B. C., Debruine, L. M., Little, A. C., Conway, C. a, & Feinberg, D. R. (2006). Integrating gaze direction and expression in preferences for attractive faces. *Psychological science*, *17*(7), 588–91. doi:10.1111/j.1467-9280.2006.01749.x

Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2004). When facial attractiveness is only skin deep. *Perception*, *33*(5), 569–576.

Jones, B. C., Little, A. C., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgements of apparent health: Support for a "'good

genes'" explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior*, *22*, 417–429.

Kampe, K. K. W., Frith, C. D., Dolan, R. J., & Frith, U. (2001). Reward value of attractiveness and gaze. *Nature*, *413*, 589. doi:10.1038/nature740

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 4302–4311.

Kanwisher, Nancy, & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *361*(1476), 2109–28. doi:10.1098/rstb.2006.1934

Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of neurophysiology*, *91*(4), 1699–705. doi:10.1152/jn.00696.2003

Kawabata, H., & Zeki, S. (2008). The neural correlates of desire. *PloS one*, *3*(8), e3027. doi:10.1371/journal.pone.0003027

Kedia, G., Mussweiler, T., Mullins, P., & Linden, D. E. J. (2013). The neural correlates of beauty comparison. *Social cognitive and affective neuroscience*. doi:10.1093/scan/nst026

Kim, H., Adolphs, R., O'Doherty, J. P., & Shimo. (2007). Temporal isolation of neural processes underlying face preference decisions. *Proceedings of the National Academy of Sciences*, *104*(46), 18253–18258.

Klein, S. L. (2000). The effects of hormones on sex differences in infection: from genes to behavior. *Neuroscience and biobehavioral reviews*, *24*(6), 627–38.

Kranz, F., & Ishai, A. (2006). Face perception Is modulated by sexual preference. *Current Biology*, *16*(1), 63–68. doi:10.1016/j.cub.2005.10.070

Kringelbach, M. L., Lehtonen, A., Squire, S., Harvey, A. G., Craske, M. G., Holliday, I. E., … Stein, A. (2008). A specific and rapid neural signature for parental instinct. *PloS one*, *3*(2), e1664. doi:10.1371/journal.pone.0001664

Kringelbach, M. L., & Radcliffe, J. (2005). The human orbitofrontal cortex: linking reward to hedonic experience. *Nature Reviews*, *6*(9), 691–702. doi:10.1038/nrn1747

Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in neurobiology*, *72*(5), 341–72. doi:10.1016/j.pneurobio.2004.03.006

Kuo, P. X., Carp, J., Light, K. C., & Grewen, K. M. (2012). Neural responses to infants linked with behavioral interactions and testosterone in fathers. *Biological psychology*, *91*(2), 302–6. doi:10.1016/j.biopsycho.2012.08.002

Kuzawa, C. W., Gettler, L. T., Huang, Y., & McDade, T. W. (2010). Mothers have lower testosterone than non-mothers: Evidence from the Philippines. *Hormones and Behavior*, *57*(4-5), 441–447. doi:10.1016/j.yhbeh.2010.01.014

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*(3), 390–423.

Langlois, J. H., Ritter, J. M., Casey, R. J., & Sawin, D. B. (1995). Infant face attractiveness affects maternal behaviours. *Developmental Psychology*, *31*(3), 464–472.

Lavi-Avnon, Y., Weller, A., Finberg, J. P. M., Gispan-Herman, I., Kinor, N., Stern, Y., … Yadid, G. (2008). The reward system and maternal behavior in an animal model of depression: a microdialysis study. *Psychopharmacology*, *196*(2), 281–91. doi:10.1007/s00213-007-0961-2

Law Smith, M. J., Deady, D. K., Moore, F. R., Jones, B. C., Cornwell, R. E., Stirrat, M. R., … Perrett, D. I. (2012). Maternal tendencies in women are associated with estrogen levels and facial femininity. *Hormones and Behavior*, *61*(1), 12–6. doi:10.1016/j.yhbeh.2011.09.005

Le, T. H., Pardo, J. V, & Hu, X. (1998). 4 T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. *Journal of neurophysiology*, *79*(3), 1535–48. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9497430

Leder, H., Tinio, P. P. L., Fuchs, I. M., & Bohrn, I. (2010). When attractiveness demands longer looks: the effects of situation and gender. *Quarterly Journal of Experimental Psychology*, *63*(9), 1858–71. doi:10.1080/17470211003605142

Lehmann, V., Huis in't Veld, E. M. J., & Vingerhoets, A. J. J. M. (2013). The human and animal baby schema effect: correlates of individual differences. *Behavioural processes*, *94*, 99–108. doi:10.1016/j.beproc.2013.01.001

Lenzi, D., Trentini, C., Pantano, P., Macaluso, E., Iacoboni, M., Lenzi, G. L., & Ammaniti, M. (2009). Neural basis of maternal communication and emotional expression processing during infant preverbal stage. *Cerebral cortex (New York, N.Y. : 1991)*, *19*(5), 1124–33. doi:10.1093/cercor/bhn153

Linn MC, Petersen AC (1985). Emergence and characterization of sex differences in spatial ability: a meta-analysis. Child Dev, 56: 1479-98.

Leonard, C., Towler, S., Welcome, S., & et al. (2008). Size matters: cerebral volume influences sex differences in neuroanatomy. *Cerebral Cortex*, *18*(12), 2920–2931.

Levenson, R. W. (2003). Blood, Sweat, and Fears. *Annals of the New York Academy of Sciences*, *1000*(1), 348–366. doi:10.1196/annals.1280.016

Levy, B., Ariely, D., Mazar, N., Chi, W., Lukas, S. E., & Elman, I. (2008). Gender differences in the motivational processing of facial beauty. *Learning and Motivation*, *39*(2), 136–145. doi:10.1016/j.lmot.2007.09.002

Liang, X., Zebrowitz, L. A., & Zhang, Y. (2010). Neural activation in the "reward circuit" shows a nonlinear response to facial attractiveness. *Social Neuroscience*, *5*(3), 320–34. doi:10.1080/17470911003619916

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution*, *62*(10), 2473–86. doi:10.1111/j.1558-5646.2008.00478.x

Little, A. C. (2012). Manipulation of Infant-Like Traits Affects Perceived Cuteness of Infant, Adult and Cat Faces. (L. Fusani, Ed.)*Ethology*, *118*(8), 775–782. doi:10.1111/j.1439-0310.2012.02068.x

Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: an MEG study. *Nature neuroscience*, *5*, 910–916.

Lobmaier, J. S., Sprengelmeyer, R. H., Wiffen, B., & Perrett, D. I. (2010). Female and male responses to cuteness, age and emotion in infant faces. *Evolution and Human Behavior*, *31*(1), 16–21. doi:10.1016/j.evolhumbehav.2009.05.004

Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung. *Zeitschrift für Tierpsychologie*, *5*(2), 235–409.

Luders, E., & Toga, A. W. (2010). Sex differences in brain anatomy. *Progress in brain research*, *186*, 3–12. doi:10.1016/B978-0-444-53630-3.00001-4

Luo, L. Z., Lee, K., & Li, H. (2011). Are children's faces really more appealing that those of adults? Testing the baby schema hypothesis beyond infancy. *Journal of experimental child psychology*, *110*(1), 115–124. doi:10.1016/j.jecp.2011.04.002.Are

Maestripieri, D., & Pelka, S. (2002). SEX DIFFERENCES IN INTEREST IN INFANTS ACROSS THE LIFESPAN A Biological Adaptation for Parenting ?, *13*(3), 327–344.

Maier, R. a., Holmes, D. L., Slaymaker, F. L., & Reich, J. N. (1984). The perceived attractiveness of preterm infants. *Infant Behavior and Development*, *7*(4), 403–414. doi:10.1016/S0163-6383(84)80002-8

Main, J. C., DeBruine, L. M., Little, A. C., & Jones, B. C. (2010). Interactions among the effects of head orientation, emotional expression, and physical attractiveness on face preferences. *Perception*, *39*(1), 62–71. doi:10.1068/p6503

Marzi, T., & Viggiano, M. (2010). When memory meets beauty: insights from event-related potentials. *Biological psychology*, *84*, 192–205.

Mascaro, J. S., Hackett, P. D., & Rilling, J. K. (2013). Testicular volume is inversely correlated with nurturing-related brain activity in human fathers. *Proceedings of the National Academy of Sciences of the United States of America*, *i*, 1–6. doi:10.1073/pnas.1305579110

Matts, P. J., Fink, B., Grammer, K., & Burquest, M. (2007). Color homogeneity and visual perception of age, health, and attractiveness of female facial skin. *Journal of the American Academy of Dermatology*, *57*(6), 977–984.

McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*, 605–610.

Mende-Siedlecki, P., Said, C. P., & Todorov, A. (2013). The social evaluation of faces: a meta-analysis of functional neuroimaging studies. *Social cognitive and affective neuroscience*, *8*(3), 285–99. doi:10.1093/scan/nsr090

Miesler, L., Leder, H., & Herrmann, A. (2011). Isn't it cute: An evolutionary perspective of baby-schema effects in visual product designs. *International Journal of Design*, *5*(3), 17–30.

Mobius, M. M., & Rosenblat, T. S. (2006). Why Beauty Matters. *The American Economic Review*, *96*(1), 222–235.

Nakamura, K., Kawashima, R., Nagumo, S., Ito, K., Sugiura, M., Kato, T., … Kojima, S. (1998). Neuroanatomical correlates of the assessment of facial attractiveness. *NeuroReport*, *9*(4), 753–757.

Nisbett, R. E., & Wilson, T. D. (1977). The halo effect: Evidence for unconscious alteration of judgments. *Journal of Personality and Social Psychology*, *35*, 250–256. doi:10.1037/0022-3514.35.4.250

Nitschke, J. B., Nelson, E. E., Rusch, B. D., Fox, A. S., Oakes, T. R., & Davidson, R. J. (2004). Orbitofrontal cortex tracks positive mood in mothers viewing pictures of their newborn infants. *NeuroImage*, *21*(2), 583–92. doi:10.1016/j.neuroimage.2003.10.005

Nittono, H., Fukushima, M., Yano, A., & Moriya, H. (2012). The power of Kawaii: viewing cute images promotes a careful behavior and narrows attentional focus. *PloS one*, *7*(9), e46362. doi:10.1371/journal.pone.0046362

Noriuchi, M., Kikuchi, Y., & Senoo, A. (2008). The functional neuroanatomy of maternal love: mother's response to infant's attachment behaviors. *Biological psychiatry*, *63*(4), 415–23. doi:10.1016/j.biopsych.2007.05.018

Numan, M, & Numan, M. (1997). Projection sites of medial preoptic area and ventral bed nucleus of the stria-terminalis neurons that express Fos during maternal behavior in female rats. *Journal of neuroendocrinology*, *9*(369-384).

Numan, Michael. (2007). Motivational Systems and the Neural Circuitry of Maternal Behavior in the Rat. *Developmental Psychobiology*, *49*(1), 12–21. doi:10.1002/dev

Nunez, JL, Jurgens, HA, & Juraska, JM (2000). Androgens reduce cell death in the developing rat visual cortex, Brain Res. Dev. Brain Res. 125, 83–88.

O'Connor, J. J. M., & Feinberg, D. R. (2012). The influence of facial masculinity and voice pitch on jealousy and perceptions of intrasexual rivalry. *Personality and Individual Differences*, *52*(3), 369–373. doi:10.1016/j.paid.2011.10.036

O'Doherty, J. P., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neuroscience*, *4*(1), 95–102. doi:10.1038/82959

O'Doherty, J. P., Winston, J. S., Critchley, H., Perrett, D. I., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147–155.

Oliver-Rodríguez, J. C., Guan, Z., & Johnston, V. S. (1999). Gender differences in late positive components evoked by human faces, 176–185.

Olson, I. R., & Marshuetz, C. (2005). Facial Attractiveness Is Appraised in a Glance. *Emotion*, *5*(4), 498–502. doi:10.1037/1528-3542.5.4.498

Parsons, C. E., Young, K. S., Kumari, N., Stein, A., & Kringelbach, M. L. (2011). The motivational salience of infant faces is similar for men and women. (G. M. McAlonan, Ed.)*PLoS ONE*, *6*(5), e20632. doi:10.1371/journal.pone.0020632

Parsons, C. E., Young, K. S., Mohseni, H., Woolrich, M. W., Thomsen, K. R., Joensson, M., … Kringelbach, M. L. (2013). Minor structural abnormalities in the infant face disrupt neural processing: A unique window into early caregiving

responses. *Social neuroscience*, *8*(4), 268–74. doi:10.1080/17470919.2013.795189

Parsons, C. E., Young, K. S., Murray, L., Stein, A., & Kringelbach, M. L. (2010). The functional neuroanatomy of the evolving parent-infant relationship. *Progressing Neurobiology, 91,* 220-241.

Parsons, C. E., Young, K. S., Parsons, E., Dean, A., Murray, L., Goodacre, T., … Kringelbach, M. L. (2011). The effect of cleft lip on adults' responses to faces: cross-species findings. *PloS one*, *6*(10), e25897. doi:10.1371/journal.pone.0025897

Pawlowski, B., & Dunbar, R. I. (1999). Impact of market value on human mate choice decisions. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1416), 281–285. doi:10.1098/rspb.1999.0634

Perrett, D I, Mistlin, a J., Chitty, a J., Smith, P. a, Potter, D. D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behavioural brain research*, *29*(3), 245–58.

Perrett, David Ian, Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *335*(1273), 23–30. doi:10.1098/rstb.1992.0003

Peters, M., Rhodes, G., & Simmons, L. W. (2008). Does attractiveness in men provide clues to semen quality? *Journal of Evolutionary Biology*, *21*(2), 572–9. doi:10.1111/j.1420-9101.2007.01477.x

Pizzagalli, D. A., Lehmann, D., Hendrick, A. M., Regard, M., Pascual-Marqui, R. D., & Davidson, R. J. (2002). Affective Judgments of Faces Modulate Early Activity (~160 ms) within the Fusiform Gyri. *NeuroImage*, *16*(3), 663–677. doi:10.1006/nimg.2002.1126

Pochon, J.-B., Riis, J., Sanfey, A. G., Nystrom, L. E., & Cohen, J. D. (2008). Functional imaging of decision conflict. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *28*(13), 3468–73. doi:10.1523/JNEUROSCI.4195-07.2008

Power, T. G., Hildebrandt, K. A., & Fitzgerald, H. E. (1982). Adults' responses to infants varying in facial expression and perceived attractiveness. *Infant Behavior and Development*, *5*(1), 33–44. doi:10.1016/S0163-6383(82)80015-5

Prestia, S., Silverston, J., Wood, K., & Zigarmi, L. (2002). The effects of attractiveness on popularity: An observational study of social interaction among college students. *Perspectives in Psychology*, (Spring), 3–11.

Proverbio, A. M. (2011). No Race Effect (ORE) in the Automatic Orienting toward Baby Faces: When Ethnic Group does not matter. *Psychology*, *02*(09), 931–935. doi:10.4236/psych.2011.29140

Proverbio, A. M., Brignone, V., Matarazzo, S., Del Zotto, M., & Zani, A. (2006). Gender and parental status affect the visual cortical response to infant facial

expression. *Neuropsychologia*, *44*(14), 2987–99. doi:10.1016/j.neuropsychologia.2006.06.015

Proverbio, A. M., Riva, F., Martin, E., & Zani, A. (2010a). Neural markers of opposite-sex bias in face processing. *Frontiers in psychology*, *1*(October), 169. doi:10.3389/fpsyg.2010.00169

Proverbio, A. M., Riva, F., Martin, E., & Zani, A. (2010b). Face coding is bilateral in the female brain. *PloS one*, *5*(6), e11242. doi:10.1371/journal.pone.0011242

Proverbio, A. M., Riva, F., Zani, A., & Martin, E. (2011). Is it a baby? Perceived age affects brain processing of faces differently in women and men. *Journal of Cognitive Neuroscience*, *23*(11), 3197–208. doi:10.1162/jocn_a_00041

Quist, M. C., DeBruine, L. M., Little, A. C., & Jones, B. C. (2012). Integrating social knowledge and physical cues when judging the attractiveness of potential mates. *Journal of Experimental Social Psychology*, *48*(3), 770–773. doi:10.1016/j.jesp.2011.12.018

Raisman G, Field PM. Sexual dimorphism in the preoptic area of the rat. Science 1971; 173: 731-3.

Ramirez, S. M., Bardi, M., French, J. a, & Brent, L. (2004). Hormonal correlates of changes in interest in unrelated infants across the peripartum period in female baboons (Papio hamadryas anubis sp.). *Hormones and behavior*, *46*(5), 520–8. doi:10.1016/j.yhbeh.2004.05.009

Ranote, S., Elliott, R., Abel, K. M., Mitchell, R., Deakin, J. F. W., & Appleby, L. (2004). The neural basis of maternal responsiveness to infants: an fMRI study. *NeuroReport*, *15*(11), 1825–1829. doi:10.1097/01.wnr.0000137078.64128.6a

Re, D. E., Hunter, D. W., Coetzee, V., Tiddeman, B. P., Xiao, D., Debruine, L. M., … Perrett, D. I. (2013). Looking like a leader-facial shape predicts perceived height and leadership ability. *PloS one*, *8*(12), e80957. doi:10.1371/journal.pone.0080957

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society B: Biological Sciences*, *270 Suppl*, S93–5. doi:10.1098/rsbl.2003.0023

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: Does attractiveness enhance mating success? *Evolution and Human Behavior*, *26*(2), 186–201. doi:10.1016/j.evolhumbehav.2004.08.014

Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Carter, V., Jones, B. C., … Petrie, M. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, *26*(3), 213–226. doi:10.1016/j.evolhumbehav.2004.09.002

Roney, J. R., Hanson, K. N., Durante, K. M., & Maestripieri, D. (2006). Reading men's faces: women's mate attractiveness judgments track men's testosterone and interest in infants. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2169–75. doi:10.1098/rspb.2006.3569

Rule, N. O., & Ambady, N. (2008). The face of success: inferences from chief executive officers' appearance predict company profits. *Psychological science*, *19*(2), 109–11. doi:10.1111/j.1467-9280.2008.02054.x

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., & Lounasmaa, O. V. (1997). Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience*, *77*(1), 49–55. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9044373

Sanefuji, W., Ohgami, H., & Hashiya, K. (2007). Development of preference for baby faces across species in humans (Homo sapiens). *Journal of Ethology*, *25*(3), 249–254. doi:10.1007/s10164-006-0018-8

Schacht, A., Werheid, K., & Sommer, W. (2008). The appraisal of facial beauty is rapid but not mandatory. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(2), 132–142. doi:10.3758/CABN.8.2.132

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1431), 1913–1917.

Seifritz, E., Esposito, F., Neuhoff, J. G., Lüthi, A., Mustovic, H., Dammann, G., … Di Salle, F. (2003). Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biological Psychiatry*, *54*(12), 1367–1375. doi:10.1016/S0006-3223(03)00697-8

Senior, C. (2003). Beauty in the brain of the beholder. *Neuron*, *38*, 525–528.

Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and physical health. *Evolution and Human Behavior*, *20*(1), 71–76. doi:10.1016/S1090-5138(98)00036-1

Shaywitz BA, Shaywitz SE, Pugh KR, Constable RT, Skudlarski P, et al. (1995) Sex differences in the functional organization of the brain for language. Nature 373: 607–609.

Sherman, G. D., Haidt, J., & Coan, J. a. (2009). Viewing cute images increases behavioral carefulness. *Emotion (Washington, D.C.)*, *9*(2), 282–6. doi:10.1037/a0014904

Smith, D. V, Hayden, B. Y., Truong, T.-K., Song, A. W., Platt, M. L., & Huettel, S. a. (2010). Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *30*(7), 2490–5. doi:10.1523/JNEUROSCI.3319-09.2010

Snyder, M., Tanke, E. D., & Berscheid, E. (1977). Social perception and interpersonal behavior: On the self-fulfilling nature of social stereotypes. *Journal of Personality and Social Psychology*, *35*(9), 656–666. doi:10.1037//0022-3514.35.9.656

Spreckelmeyer, K. N., Rademacher, L., Paulus, F. M., & Gründer, G. (2012). Neural activation during anticipation of opposite-sex and same-sex faces in heterosexual men and women. *NeuroImage*, *66C*, 223–231. doi:10.1016/j.neuroimage.2012.10.068

Sprengelmeyer, R. H., Lewis, J., Hahn, A. C., & Perrett, D. I. (2013). Aesthetic and Incentive Salience of Cute Infant Faces: Studies of Observer Sex, Oral Contraception and Menstrual Cycle. (A. Serino, Ed.)*PLoS ONE*, *8*(5), e65844. doi:10.1371/journal.pone.0065844

Sprengelmeyer, R. H., Perrett, D. I., Fagan, E. C., Cornwell, R. E., Lobmaier, J. S., Sprengelmeyer, A., … Young, A. W. (2009). The cutest little baby face: A hormonal link to sensitivity to cuteness in infant faces. *Psychological Science*, *20*(2), 149–154. doi:10.1111/j.1467-9280.2009.02272.x

Stephan, C. W., & Langlois, J. H. (1984). Baby Beautiful: Adult Attributions of Infant Competence as a Function of Infant Attractiveness. *Child Development*, *55*(2), 576–585.

Stephen, I. D., Coetzee, V., Law Smith, M. J., & Perrett, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE*, *4*(4), e5083.

Stephen, I. D., Oldham, F. H., Perrett, D. I., & Barton, R. A. (2012). Redness enhances perceived aggression, dominance and attractiveness in men's faces. *Evolutionary Psychology*, *10*(3), 562–72.

Sternglanz, S. H., Gray, J. L., & Murakami, M. (1977). Adult preferences for infantile facial features: An ethological approach. *Animal Behaviour*, *25*(1), 108–15.

Stirrat, M, & Perrett, D. I. (2010). Valid facial cues to cooperation and trust: male facial width and trustworthiness. *Psychological science*, *21*(3), 349–54. doi:10.1177/0956797610362647

Stirrat, Michael, Gumert, M., & Perrett, D. I. (2011). The effect of attractiveness on food sharing preferences in human mating markets. *Evolutionary psychology : an international journal of evolutionary approaches to psychology and behavior*, *9*(1), 79–91. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/22947957

Storey, A., Walsh, C., Quinton, R., & Wynne-Edwards, K. (2000). Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior*, *21*(2), 79–95. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10785345

Strathearn, L., Fonagy, P., Amico, J., & Montague, P. R. (2009). Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology*, *34*(13), 2655–66. doi:10.1038/npp.2009.103

Strathearn, L., Li, J., Fonagy, P., & Montague, P. R. (2008). What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics*, *122*(1), 40–51. doi:10.1542/peds.2007-1566

Swain, J. E. (2008). Baby stimuli and the parent brain: Functional neuroimaging of the neural substrates of parent-infant attachment. *Psychiatry, 5*, 28-36.

Swain, J. E., Lorberbaum, J. P., Kose, S., & Strathearn, L. (2007). Brain basis of early parent-infant interactions: psychology, physiology, and in vivo functional neuroimaging studies. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *48*(3-4), 262–87. doi:10.1111/j.1469-7610.2007.01731.x

Thorpe, S. J., Maddison, S., & Road, S. P. (1983). The Orbitofrontal Cortex : Neuronal Activity in the Behaving Monkey, *Experimental Brain Research, 49,* 93–115.

Tiedt, H. O., Weber, J. E., Pauls, A., Beier, K. M., & Lueschow, A. (2013). Sex-differences of face coding: evidence from larger right hemispheric M170 in men and dipole source modelling. *PloS one*, *8*(7), e69107. doi:10.1371/journal.pone.0069107

Tsao, D. Y., Freiwald, W. A., Tootell, R. B. H., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science (New York, N.Y.)*, *311*(5761), 670–4. doi:10.1126/science.1119983

Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences, 105*, 19514-19519.

Tsukiura, T., & Cabeza, R. (2011a). Shared brain activity for aesthetic and moral judgments: implications for the Beauty-is-Good stereotype. *Social cognitive and affective neuroscience*, *6*(1), 138–48. doi:10.1093/scan/nsq025

Tsukiura, T., & Cabeza, R. (2011b). Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces, *54*(1), 653–660. doi:10.1016/j.neuroimage.2010.07.046.Remembering

Turk, D. J., Banfield, J. F., Walling, B. R., Heatherton, T. F., Grafton, S. T., Handy, T. C., … Macrae, C. N. (2004). From facial cue to dinner for two: the neural

substrates of personal choice. *NeuroImage*, *22*(3), 1281–90. doi:10.1016/j.neuroimage.2004.02.037

van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The Steroid/Peptide Theory of social bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology, 36*, 1265-1275.

van Hooff, J. C., Crawford, H., & van Vugt, M. (2011). The wandering mind of men: ERP evidence for gender differences in attention bias towards attractive opposite sex faces. *Social cognitive and affective neuroscience*, *6*(4), 477–85. doi:10.1093/scan/nsq066

Vartanian, O., Goel, V., Lam, E., Fisher, M. L., & Granic, J. (2013). Middle temporal gyrus encodes individual differences in perceived facial attractiveness. *Psychology of Aesthetics, Creativity, and the Arts*, *7*(1), 38–47. doi:10.1037/a0031591

Volk, A. A., Lukjanczuk, J. M., & Quinsey, V. L. (2005). Influence of infant and child facial cues of low body weight on adults' ratings of adoption preference, cuteness, and health. *Infant Mental Health Journal*, *26*(5), 459–469. doi:10.1002/imhj.20064

Volk, A. A., & Quinsey, V. L. (2002). The influence of infant facial cues on adoption preferences. *Human Nature*, *13*(4), 437–455.

Waller, K. L., Volk, A. A., & Quinsey, V. L. (2004). The effect of infant fetal alcohol syndrome facial features on adoption preference. *Human Nature*, *15*(1), 101–117. doi:10.1007/s12110-004-1006-8

Walster, E., Aronson, V., Abrahams, D., & Rottman, L. (1966). Importance of physical attractiveness in dating behavior. *Journal of Personality and Social Psychology*, *4*(5), 508–516.

Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: a review. *Psychological bulletin*, *131*(5), 635–53. doi:10.1037/0033-2909.131.5.635

Weisman, O., Feldman, R., & Goldstein, A. (2012). Parental and romantic attachment shape brain processing of infant cues. *Biological psychology*, *89*(3), 533–8. doi:10.1016/j.biopsycho.2011.11.008

Weiss, M. (1994). *Conditional love: Parents' attitudes toward handicapped children* (p. 296). Westport, CT: Bergin & Garvey.

Werheid, K., Schacht, A., & Sommer, W. (2007). Facial attractiveness modulates early and late event-related brain potentials, *76*, 100–108. doi:10.1016/j.biopsycho.2007.06.008

Whitehead, R. D., Re, D. E., Xiao, D. K., Ozakinci, G., & Perrett, D. I. (2012). You are what you eat: within-subject increases in fruit and vegetable consumption confer beneficial skin-color changes. *PloS one*, *7*(3), e32988. doi:10.1371/journal.pone.0032988

Wilson, M. I., & Daly, M. (2004). Do pretty women inspire men to discount the future? *Proceedings of the Royal Society B: Biological Sciences*, *271 Suppl*, S177–9. doi:10.1098/rsbl.2003.0134

Winston, J. S., O'Doherty, J. P., Kilner, J. M., Perrett, D. I., & Dolan, R. J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, *45*(1), 195–206.

Witelson SF, Glezer II, Kigar DL. Women have greater density of neurons in posterior temporal cortex. J Neurosci 1995; 15: 3418-28.

Woll, S. B. (1986). So Many to Choose from: Decision Strategies in Videodating. *Journal of Social and Personal Relationships*, *3*(1), 43–52. doi:10.1177/0265407586031004

Yamamoto, R., Ariely, D., Chi, W., Langleben, D. D., & Elman, I. (2009). Gender differences in the motivational processing of babies are determined by their facial attractiveness. *PloS one*, *4*(6), e6042. doi:10.1371/journal.pone.0006042

Yovel, G., & Belin, P. (2013). A unified coding strategy for processing faces and voices. *Trends in cognitive sciences*, *17*(6), 263–71. doi:10.1016/j.tics.2013.04.004

Zaidi, Z. F. (2010). Gender Differences in Human Brain: A Review. *The Open Anatomy Journal*, *2*, 37–55. doi:10.2174/1877609401002010037

Zaki, J., Schirmer, J., & Mitchell, J. P. (2011). Social influence modulates the neural computation of value. *Psychological science*, *22*(7), 894–900. doi:10.1177/0956797611411057

Zebrowitz, L. A., Hall, J. A., Murphy, N. A., & Rhodes, G. (2002). Looking smart and looking good: Facial cues to intelligence and their origins. *Personality and Social Psychology Bulletin*, *28*(2), 238–249. doi:10.1177/0146167202282009

Zeng, J., Wang, Y., & Zhang, Q. (2012). An ERP study on decisions between attractive females and money. *PloS one*, *7*(10), e45945. doi:10.1371/journal.pone.0045945

Zhang, Y., Kong, F., Chen, H., Jackson, T., Han, L., Meng, J., & et al. (1995). Identifying cognitive preferences for attractive female faces: An event-related potential experiment using a study-test paradigm. *Journal of Neuroscience*, *15*, 3418–3428.

Zhang, Z., & Deng, Z. (2012). Gender, facial attractiveness, and early and late event-related potential components. *Journal of integrative neuroscience*, *11*(4), 477–87. doi:10.1142/S0219635212500306